Title: Maize production in a changing climate: Impacts, adaptation and mitigation strategies

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Abstract
Plant breeding and improved management options have made remarkable progress in increasing crop yields during the past century. However climate change projections suggest large yield losses will be occur in many regions, particularly within sub-Saharan Africa. The development of climate-ready germplasm to offset these losses is of the upmost importance. Given the time lag between the development of improved germplasm and adoption in farmers' fields, the development of improved breeding pipelines needs to be a high priority. Recent advances in molecular breeding provide powerful tools accelerate breeding gains and dissect stress adaptation. This review focuses on achievements in stress tolerance breeding and physiology and presents future tools for quick and efficient germplasm development. Sustainable agronomic and resource management practices can effectively contribute to climate change mitigation. Management options to increase maize system resilience to climate-related stresses and mitigate the effects of future climate change are also discussed.

1. Introduction
Maize is produced on nearly 100 million hectares in developing countries, with almost 70 % of the total maize production in the developing world coming from low and lower middle income countries (FAOSTAT, 2010). By 2050 demand for maize will double in the developing world, and maize is predicted to become the crop with the greatest production globally, and in the developing world by 2025 (Rosegrant *et al.,* 2008). In large parts of Africa maize is the principle staple crop; accounting for an average of 32 % of consumed calories in Eastern and Southern Africa, rising to 51 % in some countries (Table 1). Heisey and Edmeades (1999) estimated that one quarter of the global maize area is affected by drought in any given year. Additional constraints causing significant yield and economic losses annually include low soil fertility, pests and disease. It is difficult to give an accurate figure on combined maize yield losses due to these stresses, however it is likely to be extensive. Maize yields remain low and highly variable between years across sub-Saharan Africa at 1.6 t ha^{-1}, only just enough to reach self-sufficiency in many areas (Bänziger and Diallo, 2001; FAOSTAT, 2010). The world population is expected to surpass 9 billion by 2050, with population growth highest within developing countries. Harvest at current levels of productivity and population growth will fall far short of future demands. Projections of climate change will further exacerbate the ability to ensure food security and foster economic growth within many maize producing areas. The development of improved germplasm to meet the needs of future generations in light of climate change and population growth is of the upmost importance (Easterling *et al.,* 2007).

Past experience has demonstrated that the use of new varieties alongside improved management options can offset yield losses by up to 40% (Thornton et al. 2009). The development and application of molecular tools in plant breeding started in the early 1980's. Molecular breeding offers the ability to increase the speed and efficiency of plant breeding (Whitford *et al.,* 2010). In rice, *SUB1* a major QTL controlling submergence tolerance was recently identified and introgressed into local mega varieties using only two backcrosses and one selfing generation (Septiningsih *et al.,* 2009). In maize a gene encoding β-carotene (crtRB1) was recently identified and is now being introgressed into tropical germplasm using marker assisted selection to alleviate vitamin A deficiency in the developing world (*Yan et al.,* 2010). Many more examples of the use of molecular tools to quickly develop improved germplasm

with resilience to major abiotic and biotic stress are beginning to emerge. As the impacts of climate change will vary regionally, and given the time lag between the development of improved germplasm and adoption in farmers' fields, there is an immediate need to identify future breeding target environments and reduce uncertainty within climate projections to allow priority setting for both researchers and policy markers.

This review addresses the potential impacts of climate change on maize production with specific reference to sub-Saharan Africa. Considerable gaps remain in our knowledge of how agricultural systems will be affected. Earlier climate projections have tended to focus at the country level. While these studies have helped to increase our understanding of potential future climates, at such low resolution priority setting of agricultural research is not possible. Climate projections for sub-Saharan Africa at the maize mega-environment level within countries are presented. Current research and potential new tools to increase maize resilience to abiotic and biotic stresses are presented. Finally mitigation technologies and practices for maize-based systems are discussed.

2. Likely climate scenarios for sub-Saharan Africa and South Asia and identification of hot spots

Previously climate projections were developed using the outputs of few global climate models (GCMs) at low resolution. Large variation exists within the outputs of GCMs and for regional application the use of multiple models reduces the error in both the mean and variability. Additionally, the earlier focus on low resolution modeling at the country level masks large variation in key factors, such as climate and topography, and reduces the potential application of projections as decision making tools for identifying priority areas for research. Working at the regional level, Thornton *et al.,* (2009) showed large spatial variation in simulated yield production changes of maize and beans within the highlands of Ethiopia and Kenya. There is a pressing need to identify future breeding targets and hot-spots of vulnerability to climate change in maize growing areas.

The CIMMYT maize breeding program is organized around the concept of mega-environments, or areas with broadly similar environmental characteristics with respect to maize production, to target its breeding programs. Mega-environments were delineated using environmental factors (maximum temperature, rainfall and sub-soil pH), as explanatory factors for genotype by environment interaction of advanced hybrids from multi-environmental trials (Setimela *et al.,* 2005, Banziger *et al.,* 2006). Similar combinations of climatic and edaphic conditions exist within and across continents, allowing maize mega-environments to be approximately identified on the basis of GIS data. Six maize mega-environments were identified across sub-Saharan Africa (Figure 1) and South and South-East Asia (Figure 2), respectively. Germplasm developed at key sites within mega-environments should have broad adaptation across the mega-environment. As climatic conditions change at particular experimental sites and maize producing regions, mega-environment assignments will need to be re-assessed to guide breeders to appropriate new germplasm and target environments. CIMMYT's global maize breeding programs can rapidly source elite, potentially useful germplasm from the full range of mega-environments in the developing world. Although it should be noted that end-use characteristics, color preferences, and other factors may often prevent the direct substitution of, say, lowland-adapted varieties for varieties in mid-elevation mega-environments that are experiencing warming. Thus, in

addition to being able to source germplasm from mega-environments with conditions similar to those arising from climate change in their own areas, breeders will need the capacity to rapidly move stress tolerance traits into germplasm preferred by people in the target environment they serve.

Previous research strongly suggests maize growing regions of sub-Saharan Africa will encounter increased growing season temperatures and frequency of droughts (IPCC, 2007). To establish changes in maximum temperatures and annual rainfall difference at the maize mega-environment level within countries, downscaled outputs from 19 SRES (Special Report on Emissions Scenarios) models and the A2 emissions scenario with data provided by CIAT (Ramirez and Jarvis, 2008) were used with the following climate change models: BCCR-BCM 2.0, CCCMA-CGM2, CCCMA-CGCM3.1 T47, CCCMA-CGCM3.1 T63, CNRM-CM3, IAP-FGOALS-1.0G, GISS-AOM, GFDL-CM2.1, GFDL-CM2.0, CSIRO-MK3.0, IPSL-CM4, MIROC 3.2-HIRES, MIROC 3.2-MEDRES, MIUB-ECHO-G, MPI-ECHAM5, MIUB-ECHO-G, MPI-ECHAM5, MRI-CGCM2.3.2A., NCAR-PCM1, NIES99, UKMO-HADCM3. Countries were sub-divided into maize mega-environments as shown in Figures 1 and 2. For temperature and precipitation projections the period 2040 to 2069 was selected, average temperatures and annual precipitation during this period are presented and referred to as 2050. Climatic data was downscaled to approximately 5 m resolution and the relationship between historical climate data from meteorological stations and climate model outputs was established using an empirical statistical approach. Average temperatures were derived from the combined outputs of all 19 models using ArcGIS software (Ormsby *et al.,* 2009). The differences between future predictions and current long-term average values (1950-2000) were calculated using the worldclim 1.4 dataset also at 2.5min resolution as a reference (Hijmans *et al.,* 2005). Values within mega environments within the respective countries were averaged.

The results of temperature simulations for 2050 across maize mega environments within sub-Saharan Africa show a general trend of warming, in agreement with previous projections conducted at the country level (IPCC, 2007; Burke *et al.,* 2009) (Figure 3). In sub-Saharan Africa warming is the greatest over central southern Africa and western semi-arid margins of the Sahara and least in the coastal regions of West Africa. Maximum temperatures are predicted to increase by 2.6 °C, with the increase in minimum temperatures slightly lower, with an average of 2.1 °C. In agreement with Burke *et al.,* (2009), the range of temperatures within a country is likely to be larger than the range of temperatures across years (2010-2050). Average optimum temperatures in temperate, highland tropical and lowland tropical maize lie between 20-30 °C, 17-20 °C, and 30–34 °C, respectively (Badu-Apraku, 1983; Brown, 1997; Chang, 1981; Chowdhury and Wardlaw, 1978). Maximum temperatures currently exceed optimal temperature conditions for lowland tropical maize (34 °C) within several countries (Burkina Faso, Chad, Eritrea, Gambia, Mali, Mauritania, Niger, Nigeria, Senegal and Sudan) although the area of maize grown within several of these regions is small. Maize is an important crop in the highlands of Kenya, Ethiopia and Tanzania. Average temperatures within these regions are currently at the threshold for highland maize and will likely exceed this threshold by 2050.

Projections of changes in precipitation show a general trend of increased annual precipitation in western and eastern Africa. In general, annual precipitation is projected to decrease within Malawi, Madagascar, north-east South Africa, Angola, Gabon, Cameroon and Congo. Annual rainfall in

Cameroon, Congo and Gabon is relatively high with an average of 1504, 1475 and 1564 mm rainfall annually, respectively (calculated from 1995 to 2005 rainfall data from Mitchell and Jones, 2005). Therefore the decrease in rainfall may not have a major impact on maize production within these countries. Decreasing precipitation combined with increasing temperatures may have major implications for maize production within Mozambique, South Africa and Madagascar. These results highlight potential hotspots for targeting research, however further refinement is required to decipher potential changes in precipitation during the growing season (particularly during the reproductive stage) and potential impacts of combined changes including heat and drought stress combined. Given the projected changes in temperature and precipitation, two of the main environmental factors used to delineate current maize mega-environments, it is likely some regions will have to be reclassified into new mega-environments or a new environmental classification system developed. Ortiz *et al.* (2008) previously examined potential changes in major wheat production environments as a result of climate change using one GCM. The results of their study suggest up to 51 % of the wheat regions within the Indo-Gangetic Plains would need to re-classified.

3. Adaptation technologies and practices for addressing near-term and progressive climate change

3.1. Abiotic stresses – drought, heat and waterlogging

3.1.1. Drought

Drought is a widespread phenomenon across large areas of sub-Saharan Africa, with an estimated 22 % of mid-altitude/subtropical and 25 % of lowland tropical maize growing regions affected annually inadequate water supply during the growing season (Heisey and Edmeades, 1999). In Eastern and Southern Africa, a general relationship can be observed between annual rainfall and national average maize yields (Figure 5) (Bänziger and Diallo, 2001). Conventional drought stress tolerance breeding has yielded significant dividends in maize (Bänziger *et al.,* 2006). Conventional breeding for drought tolerance has resulted in gains of up to 144 kg ha^{-1} yr^{-1} in tropical maize when stress was imposed at flowering (Edmeades *et al.,* 1999). In temperate maize, the rate of breeding progress has been estimated at 73 kg ha^{-1} yr^{-1} for mild stress (Duvick, 1997), 146 kg ha^{-1} yr^{-1} when the stress was imposed at the flowering stage, and 76 kg ha^{-1} yr^{-1} when the stress was imposed during mid-grain filling stage (Campos *et al.,* 2004). Success in breeding drought tolerant tropical maize, has been largely attributed with the application of proven drought breeding methodologies in managed stress screening (Bänziger *et al.,* 2006).

While drought negatively affects all stages of maize growth and production, the reproductive stage, particularly between tassel emergence and early grain-filling, is the most sensitive to drought stress (Grant *et al.,* 1989). Drought stress during this period results in a significant reduction in grain yield, associated with a reduction in kernel size (Bolaños and Edmeades, 1993). The susceptibility of maize to drought stress is generally attributed to its separation of male and female flowers (Grant *et al.,* 1989). While silking is delayed under drought stress, there is little effect on the timing of pollen shed. Comparisons of the responses of male and female reproductive tissues under drought stress confirmed female tissues to be the most sensitive (Moss and Downey, 1971; Herrero and Johnson, 1983). Westgate and Boyer (1986) compared the response of male and female reproductive tissues and found silk water potential to follow changes in leaf water potential, while pollen water potential remained unchanged.

The results of their experiments indicated stigmatic tissues were in moderate hydraulic contact with vegetative tissue. Using stem infusions of sucrose solution, Boyle *et al.* (1990) showed that the effects of drought at flowering could be partially alleviated; suggesting silk delay may be a symptom of limited assimilates supply rather than a primary cause of bareness. The delay in silking results in decreased male-female flowering synchrony or increased anthesis-silking interval (ASI). Early field experiments reported an 82 % reduction in grain yield as ASI increased from 0 to 28 days (DuPlessis and Dijkhuis, 1967, as reported in Edmeades *et al.,* 1993).

In the 1970's CIMMYT initiated a drought breeding program for maize using the elite lowland tropical maize population "Tuxpeño Sequia" (Bolanos and Edmeades, 1993a and b; Bolanos *et al.,* 1993). A recurrent selection approach was applied to increase the frequency of alleles conferring tolerance. Evaluations were conducted under managed drought stress imposed at flowering with selection for grain yield, increased flowering synchrony and delayed leaf senescence (Bolaños and Edmeades, 1993a). Drought stress reduced grain yield by an average of 15 to 30 % relative to the well-watered control. Over eight cycles of full-sib recurrent selection the drought tolerance of Tuxpeño Sequia was improved. Selection gains were associated with reduced ASI, fewer barren plants, a smaller tassel size, a greater harvest index, and delayed leaf senescence, with no changes in water uptake or biomass observed (Bolaños *et al.,* 1993; Bolaños and Edmeades, 1993a and b; Chapman and Edmeades, 1999). Root biomass decreased by one-third in the top 50 cm (Bolaños *et al.,* 1993). Retrospective studies were conducted on hybrids selected to represent yield improvements from the 1950's to 1980's in temperate maize (Tollenaar and Lee, 2006; Tollenaar and Wu, 2009) showed yield improvements were associated with more efficient resource capture and use of resources, particularly under stress.

New secondary traits and phenotyping methods will help to continue the success of drought tolerance breeding for tropical maize. Yield is a function of many processes throughout the plant cycle thus integrative traits that encompass crop performance over time or organization level (i.e. canopy level) will provide a better alternative to instantaneous measurements which only provide a snapshot of a given plant process (Araus *et al.,* 2008). Many new phenotyping tools based on remote sensing are now available including non-destructive measurements of growth-related parameters based on spectral reflectance (Marti *et al.,* 2007) and infrared thermometry to estimate plant water status (Jones *et al.,* 2009). Recently Cabrera-Bosque *et al.* (2009a; 2009b) proposed oxygen isotope enrichment ($\Delta^{18}O$) and kernel ash content as new physiological traits to improve maize yields in drought-prone environments. Both traits provide an integrative measurement of physiological traits during the crop growth cycle, with $\Delta^{18}O$ reflecting plant evaporative conditions throughout the crop cycle (Barbour *et al.,* 2000) while kernel ash content provides information on integrative photosynthetic and retranslocation processes during grain filling (Araus *et al.,* 2001). Together these tools have potential to be used in the characterization and identification of key drought tolerant donors to be used in breeding programs. However further work is required to evaluate their possible application as selection tools within drought breeding programs.

3.1.2. Heat

By the end of this century, growing season temperatures will exceed the most extreme seasonal temperatures recorded in the past century (Battisti and Naylor, 2009). Using crop production and meteorological records, Thomson *et al.,* (1966) showed that a 6 °C increase in temperature during the grain filling period resulted in a 10% yield loss in the US Corn Belt. A later study in the same region showed maize yields to be negatively correlated with accumulated degrees of daily maximum temperatures above 32 °C during the grain filling period (Dale, 1983). Lobell and Burke (2010) suggested that an increase in temperature of 2 °C would result in a greater reduction in maize yields within sub-Saharan Africa than a decrease in precipitation by 20 %. A recent analysis of more than 20,000 historical maize trial yields in Africa over an eight year period combined with weather data showed for every degree day above 30 °C grain yield was reduced by 1 % and 1.7 % under optimal rainfed and drought conditions, respectively (Lobell *et al.,* 2011). These reports highlight the need to incorporate tolerance to heat stress into maize germplasm. However, relatively little research has been conducted on heat stress compared to other abiotic stresses in maize (Paulsen, 1994). The vast majority of heat stress research has been conducted on temperate maize germplasm for high production areas. Therefore, limited breeding progress has been made in the development of improved maize germplasm with specific tolerance to elevated temperatures. Heat stress can be defined as temperatures above a threshold level that results in irreversible damage to crop growth and development and is a function of intensity, duration and the rate of increase in temperature. Furthermore, different plant tissues and organs, and different developmental stages are affected by heat stress in different ways, depending on the susceptibility of the dominant metabolic processes that are active at the time of stress (Larkindale *et al.,* 2005). Accumulated or acute high temperatures can cause an array of morphological, anatomical, physiological and biochemical changes within maize. The threshold temperature for maize varies across environments as previously described in Section 2. The most significant factors associated with maize yield reduction include shortened life cycle, reduced light interception and increased sterility (Stone, 2001). To stabilize maize yields under elevated temperatures it is necessary to understand the mechanisms responsible for yield loss.

The temperature threshold for damage by heat stress is significantly lower in reproductive organs than in other organs (Stone, 2001). Successful grain set in maize requires the production of viable pollen, interception of the pollen by receptive silks, transmission of the male gamete to the egg cell, initiation and maintenance of the embryo and endosperm development (Schoper *et al.,* 1987). High temperature during the reproductive phase is associated with a decrease in yield due to a decrease in the number of grains and kernel weight. Under high temperatures, the number of ovules that are fertilized and develop into grain decreases (Schoper *et al.,* 1987a and b). A comparison of the response of male and female reproductive tissues to heat stress demonstrated that female tissues have greater tolerance (Dupis and Durnas, 1990). Pollen production and/or viability have been highlighted as major factors responsible for reduced fertilisation under high temperatures. Pollen produced under high temperature has reduced viability and *in vitro* germination (Herrero and Johnson, 1980; Schoper *et al.,* 1986; Schoper *et al.,* 1987a and b; Dupis and Durnas, 1990). Additionally, high temperatures are responsible for reduced pollen water potential, quantity of the pollen shed and pollen tube germination (Schoper *et al.,* 1987; Dupis and Durnas, 1990). Pollen desiccated to 20 % of its original water content is still capable of germination (Barnabas, 1985); thus, the reduction in pollen water potential under heat

stress is unlikely to be the cause of reduced pollen viability (Schoper *et al.,* 1987b), The location of the tassel also provides maximum exposure to extreme temperatures, increasing the probability of pollen damage as a result of heat stress.

High temperature during the early stages of kernel development has a detrimental effect on kernel development and final kernel mass due to a reduction in the number and/or size of endosperm cells formed thereby reducing sink capacity (Jones *et al.,* 1984). During this stage heat stress affects cell division, sugar metabolism and starch biosynthesis, reducing subsequent dry matter accumulation within kernels (Commuri and Jones, 2001; Engelen-Eigles *et al.,* 2000; Monjardino *et al.,* 2005). The duration of the grain filling process (ca. 35 days) is the longest physiological process during the reproductive stage, increasing the probability of experiencing high temperature during this stage. Maize kernel weight is the product of the rate and duration of grain filling, both of which are affected by temperature. High temperature during this period is associated with a reduction in the duration of grain filling (Hunter *et al.,* 1977; Badu-Apraku *et al.,* 1983; Muchow, 1990). Earlier studies showed temperature to increase the growth rate of kernel development (Singletary *et al.,* 1994; Muchow, 1990); however, this increase was unable to compensate for the reduction in growth duration and this resulted in kernels that weigh less (Singletary *et al.,* 1994). When the rate and duration of grain filling are calculated on the basis of accumulated heat units, the greatest reduction is in the rate, and not the duration of grain filling. Thus, the larger reduction in the rate of grain filling was responsible for the heat-related reduction in seed mass (Wilhelm *et al.,* 1999).

Grain filling duration is determined by a number of factors including sucrose availability and the activity of starch and sugar metabolism enzymes in the kernel (Jones *et al.,* 1984). Heat stress during grain filling reduces endosperm starch content, the primary constituent of kernels (Singletary *et al.,* 1994). Cheihk and Jones (1994) studied the effect of heat stress (35 °C) on sink activity of maize kernels *in vitro*. Heat stress was not associated with reduced carbon supply to the kernel, suggesting that the effect of heat stress was related to changes in carbon utilization and partitioning. Thus, heat stress did not reduce sink activity by reducing kernel uptake of sugars but by adversely affecting the conversion of sugars to storage products. *In vitro* studies on the effects of high temperature on carbohydrate metabolism enzymes in maize kernels suggest ADP glucose pyrophosphorylase and sucrose synthase to be the most sensitive with developmental peaks of activity similar to profiles of starch accumulation (Keeling *et al.,* 1994; Singletary *et al.,* 1994; Wilhelm *et al.,* 1999).

Elevated temperatures also negatively affect the seedling and vegetative stages. During the autotrophic phase of germination, plant energy is directly affected by soil temperature (Stone, 2001). High temperature reduces both seedling percentage and growth (Weaich *et al.,* 1996a). In maize, seedling growth is maximized at a soil temperature of 26 °C and above this temperature, root and shoot mass both decline by 10 % for each degree increase until 35 °C when growth is severely retarded (Walker, 1969). Reduced seedling growth has been suggested to be associated with poor reserve mobilization, with reduced protein synthesis observed in seedlings grown under elevated temperatures (Riley, 1981). Seedlings growing in high soil temperatures are likely to suffer further damage as the associated slower growth rate delays canopy closure, consequently reducing soil shading. Above 35 °C,

maize leaf elongation rate, leaf area, shoot biomass and photosynthetic CO_2 assimilation rate decreases (Watt, 1972). Elongation of the first internode and overall shoot growth of maize has been suggested as the most sensitive processes of the vegetative stage to high temperatures (Weaich *et al.,* 1996b). C_4 plants have a higher optimum temperature for photosynthesis compared to C_3 plants due to the operation of a CO_2-concentrating system that inhibits rubisco oxygenase activity (Berry and Björkman, 1980). However a comparison of the photosynthetic responses and sensitivity of the light reactions in both C_3 and C_4 crop plants subjected to brief heat stress suggested that the C_4 pathway alone did not necessarily confer tolerance to high temperature (Ghosh *et al.,* 1989). Differences in photosynthetic response were more closely associated with light reactions, particularly the sensitivity of photosystem II activity under elevated temperatures.

Research to date on specific tolerance to heat stress in maize has mainly focused on biochemical and molecular responses using only a limited number of accessions and heat stress applied *in vitro* as a single, rapid heat stress event. In wheat, progressive heat stress has a more deleterious effect on yield and yield components when compared to a single, rapid event of heat stress (Corbellini *et al.,* 1997). In maize, no comparisons have been made between rapid heat treatments (*in vitro* and field) and progressive heat stress, as commonly experienced in the field. Given that different traits and mechanisms are likely to provide adaptation for different types of heat stress (i.e. varying in duration, intensity and timing), heat stress environments need to be defined to enable the assessment of the relevance of individual physiological and breeding experiments for the target populations of environments.

3.1.3. Waterlogging

Over 18 % of the total maize production area in South and Southeast Asia is frequently affected by floods and waterlogging problems, causing production losses of 25–30 % annually (Zaidi *et al.,* 2010) (Figure 6). Although the area of land in sub-Saharan Africa affected by waterlogging is lower than in Asia, it is a risk in a few areas (Figure 7). Waterlogging stress can be defined as the stress inhibiting plant growth and development when the water table of the soil is above field capacity. The diffusion rate of gases in the flooded soil could be 100 times lower than that in the air, leading to reduced gas exchange between root tissues and the atmosphere (Armstrong and Drew, 2002). As a result of the gradual decline in oxygen concentration within the rhizosphere, the plant roots suffer hypoxia (low oxygen), and during extended waterlogging, (more than 3 days) anoxia (no oxygen) (Zaidi *et al.,* 2010). Carbon dioxide, ethylene and toxic gases (hydrogen sulphide, ammonium and methane) also accumulate within the rhizosphere during periods of waterlogging (Ponnamperuma, 1984). A secondary effect of waterlogging is a deficit of essential macronutrients (nitrogen, phosphorous and potassium) and an accumulation of toxic nutrients (iron and magnesium) resulting from decreased plant root uptake and changes in redox potential. Nutrient uptake is reduced as a result of several factors. Anaerobic conditions reduce ATP production per glucose molecules, thereby reducing energy available for nutrient uptake. Reduced transport of water further reduces internal nutrient transport. Reduced soil conditions decrease the availability of key macro nutrients within the soil. Under waterlogging conditions nitrate is reduced to ammonium and sulfate is converted to hydrogen sulphide, and both become unavailable to

most of the non-wetland crops, including maize. Availability of phosphorous may increase or decrease depending upon soil pH during waterlogging.

The extent of damage due to waterlogging stress varies significantly with the developmental stage of the crop. Previous studies have shown that maize is comparatively more susceptible to waterlogging from the early seedling stage to the tasseling stage (Mukhtar *et al.,* 1990; Zaidi *et al.,* 2004). The effects of waterlogging result in a wide spectrum of changes at the molecular, biochemical, physiological, anatomical and morphological levels, and such changes have been extensively reviewed (Kennedy *et al.,* 1992; Perata and Alpi, 1993; Ricard *et al.,* 1994). The first symptoms of waterlogging are leaf rolling and wilting and reduced stomatal conductance. These changes are followed by root growth inhibition, changes in root and shoot morphology, change in root to shoot ratio, leaf senescence and brace root development by above ground nodes (Rathore *et al.,* 1998; Zaidi and Singh, 2001; Zaidi *et al.,* 2002, 2003). Rapid wilting is related to water deficit due to net loss of water from shoot, which might be related to increased resistance to water flow in roots (Levitt, 1980). In maize, decrease in water availability under waterlogging was found to be associated with root decay and wilting. Reduced stomatal conductance and high humidity causes a reduced demand on the root system for water acquisition. Leaching-induced disturbance in the osmotic gradient of the root cortex results in inhibition of radial movement of water from root hairs across the cortex into xylem. Consequently, the water supply to above ground plant parts is reduced and plants suffer internal drought stress.

A sharp decline in aerobic respiration in root tissues is one of the earliest responses of plants under waterlogging. Waterlogging-induced anaerobiosis results in energy starvation, with only 2 ATP produced per mole of glucose, coupled with the production of toxic end products (ethanol, lactate, malate, alanine). Zaidi *et al.,* (2003) found that NAD+-alcohol dehydrogenase activity increased exponentially in the tolerant maize genotypes under waterlogging with a decline in ADH-activity in sensitive genotypes. Sachs (1993) analyzed waterlogging tolerance in maize and found that ADH-activity was apparent within 90 min and reached its highest level after approximately 5.0 hrs of the anoxia treatment. They concluded that variation in the stress tolerance was related the ADH-activity. However, Liu *et al.,* (1991) suggested that increased alcoholic fermentation was a temporary adaptation and a major cause of root injury during flooding, and flooding tolerance was related to low ethanol fermentation. Liao and Lin (1995) also suggested that ADH activity was positively correlated with the magnitude of excess moisture injury, and genotypes with higher ethanol production were less tolerant to flooding. It has been proposed that ethanol accumulation may have a “self poisoning” role in flood-intolerant plants. Plant roots under waterlogging conditions require a large amount of carbohydrate due to inefficient anaerobic respiration. Increased anerobic respiration results in rapid depletion of carbohydrate in roots, causing “carbohydrate starvation” during periods of waterlogging (Setter *et al.,* 1987).

Poorly developed brace roots before tasseling have been suggested as an important factor for increased susceptibility during the vegetative growth (Rathore *et al.,* 1998; Zaidi *et al.,* 2003). At later growth stages, some genotypes have the ability to produce adventitious roots with aerenchyma formation in the cortical region, thereby increasing the ability to tolerate excess water within the

rhizosphere (Rathore *et al.,* 1998; Zaidi, 2003). Under extended waterlogging (>3 days) formation of lysigenous aerenchyma in the cortical region of roots and brace root development on above ground nodes has been observed in waterlogging tolerant maize genotypes (Rathore *et al.,* 1998; Zaidi and Singh 2001, 2002; Zaidi *et al.,* 2003; Mano *et al.,* 2005, 2007). In maize, production of adventitious roots with aerenchyma is not a constitutive but an adaptive trait, particularly under waterlogging conditions. Aerenchyma are formed through ethylene-induced cell lysis, a process of progressive cell deterioration or precocious senescence (Jackson *et al.,* 1989; Jackson, 1990; Vartapetian and Jackson, 1997). Aerenchyma provide a diffusion path of low resistance for the transport of oxygen from aerial parts of the newly developed brace root to the roots present under severe anoxic conditions (Kawase and Whitmoyer, 1980; Laan *et al.,* 1989). They also provide a path for diffusion of volatile compounds such as ethylene, methane, CO2, ethanol, and acetaldehyde (Visser *et al.,* 1997; Vartapetian and Jackson, 1997).

Significant genotypic variation has been observed for tolerance to flooding in maize (Rathore *et al.,* 1998; Zaidi and Singh, 2001; Zaidi *et al.,* 2003). This variability could be exploited to develop maize varieties tolerant to intermittent waterlogging stress during the summer-rainy season in the tropics. In the 1980's EMPBRAPA in Brazil initiated a breeding program for waterlogging tolerance in maize (Ferreira *et al*., 2007). Recurrent selection over 12 cycles resulted in the development and subsequent release of the waterlogging tolerant BRS 4154 maize line, with a 20 % yield advantage under waterlogging compared to the original source. The results of this long term breeding effort highlight the potential to develop improved maize germplasm with tolerance to waterlogging and, in addition, the time investment required under conventional breeding.

3.2. Biotic stresses of maize under the changing climate

Abiotic stresses account for a significant proportion of maize yield losses worldwide. The predominant insect-pests and diseases vary across environments (Table 2) and a major challenge in adapting crops to climate change will be the maintenance of genetic resistance to pests and diseases (Reynolds and Ortiz, 2010). Changing climates will affect the diversity and responsiveness of agricultural pests and diseases. Studying and understanding the drivers of change will be essential to minimize the impact of plant diseases and pests on maize production.

3.2.1. Plant diseases

For a disease to occur a virulent pathogen, susceptible host and favourable environment are essential (Legrève and Duveiller, 2010). All of these components are strongly coupled with environmental conditions. Global climate changes have the potential to modify host physiology and resistance, and alter both stages and rates of pathogen development. Environmental conditions controlling disease development include rainfall, relative humidity, temperature and sunlight. Changes in these factors under climate change are highly likely to have an effect on the prevalence of diseases and emergence of new diseases. For example, in Latin America tar spot complex, caused by *Phyllachora maydis* Maubl., *Monographella maydis* Müller & Samuels and *Coniothyrium phyllachorae*, was previously rare. However, recent epidemics of the tar spot complex have been recorded in Guatemala, Mexico, Colombia and El Salvador due to recent climate variability (Pereyda-Hernández *et al.,* 2007).

The disease infection cycle includes inoculum survival, infection, latency period, production of new propagules and dispersal, all of which are strongly influenced by environmental conditions. The penetration or infection of a plant by infectious propagules is determined by specific environmental conditions. In general, fungi require high relative humidity or moist leaf surfaces for infection; changes in these conditions will increase infection rates. For example, *Cercospora zeae-maydis* and *Cercospora zeina* cause gray leaf spot (GLS) in maize and are highly sensitive to environmental conditions (Crous *et al.,* 2006). Under dry conditions (relative humidity < 80%), the pathogen ceases to grow and infection stops (Thorson and Martinson, 1993). Therefore, changes in temperature, humidity and rainfall patterns have the potential to increase infection by many maize pathogens. Increased temperature reduces the latency period (generation time) resulting in a higher number of generations per season. Generation time determines the amplification of plant disease in two ways – accelerating and increasing inoculums load and/or affecting pathogen evolution rates and a pathogen's capacity to adapt to the environment – potentially allowing the pathogen to adapt faster to the environment than the host.

Climate change may also affect gene flow, the process through which particular alleles or individuals are exchanged among separate populations. This will increase pathogen population diversity leading to variation in host resistance, variation in pathogen virulence and new specific interactions. This has the potential to result in new diseases or pathogen emergence, and the introduction of pathogens into new ecological niches. Depending on the distribution of populations and environmental conditions that are influenced by climate change, gene flow leads to an increase in population diversity or to the introduction of a new population in new ecological niches.

An important example of changes in growing season conditions being linked to outbreaks of diseases, with serious human health implications, is mycotoxins and their prevalence within maize systems. Mycotoxins are toxic secondary fungal metabolites that contaminate agricultural products and threaten food safety. Different groups of mycotoxins are produced by different fungi. *A. flavus* and *A. parasiticus* produce aflatoxin, *F. verticillioides* produces fumonisin, and *F. graminierum* produces deoxynivelanol (DON) and zearalenone) (Cardwell *et al.,* 2001; Miller, 2008). Mycotoxin contamination is a serious problem with long-term consequences for human and animal health. Sub-lethal exposure to mycotoxins suppress the immune system, increase the incidence and severity of infectious diseases, reduce child growth and development, and reduce the efficacy of vaccination programs (Williams *et al.,* 2004). Consumption of high doses of mycotoxins causes acute illness and can prove fatal. In 2004, more than 125 people died in Kenya from eating maize with aflatoxin B1 concentrations as high as 4,400 parts per billion - 220 times the Kenyan limit for foods (Lewis *et al.,* 2005). The maize implicated in this outbreak was harvested during unseasonable early rains and stored under wet conditions conducive to mold growth and therefore aflatoxin contamination (CDC, 2004). Previous outbreaks in Kenya and India have also been attributable to unseasonable, heavy rain during harvest (Krishnamachari *et al.,* 1975; Ngindu *et al.,* 1982). Environmental conditions conducive to mycotoxin producing fungi vary. *A. flavus* competes poorly under cool conditions and the prevalence of *A. flavus* is higher in warmer environments (above 25°C) compared to cooler environments (20 - 25 °C) (Shearer *et al.,* 1992). The environment influences not only the quantity of aflatoxin producers, but also the "type" of producer

present (Horn & Dorner, 1999). In Africa, the "S" mophotypes of *A. flavus* are associated with hot and dry 'agro-ecological zones with latitudinal shifts in climate influencing fungal community structure (Cardwell & Cotty, 2002). For the Fusariums, *F. graminearum,* is predominate in temperate maize growing environments, whereas *F. verticillioides* and *F. proliferatum* and fumonisins are more widely spread in tropical and subtropical environments (Miller, 1994). The optimal temperature range for *F. graminearum* is between 24-28 °C and above this temperature range *F. verticillioides* out-competes *F. graminearum* (Miller, 2001; Reid *et al.,* 1999). Increasing temperatures within maize growing regions are highly likely to change the geographical distribution and predominance of *F. verticillioides*, particularly in currently cooler regions where it will replace *F. graminerum*. This shift in *Fusarium* species will result in a change in mycotoxins, from deoxynivalenol and zearalenone (produced by *F. graminierum)* to fumonisin (produced by *F. verticillioides*). Increased incidence of *F. verticillioides* and subsequent fumonisin contamination has already been reported in Guatemala, Mexico, Zimbabwe and Kenya (Torres *et al.,* 2007).

3.2.2. Insect-pests

The dynamics of insect-pests are also strongly coupled with environmental conditions. Insects do not use their metabolism to maintain their body temperature, and are dependent on ambient temperature to control their body temperature. Temperature is therefore the single most important environmental factor influencing insect behavior, distribution, development and survival, and reproduction. Insect life stage predictions are calculated on accumulated degree days, which is a function of both time and temperature. Increased temperature can speed up the life cycle of insects leading to a faster increase in pest populations. It has been estimated that a 2 °C increase in temperature has the potential to increase the number of insect life cycles during the crop season by one to five times (Petzoldt and Seaman, 2005;, Bale *et al.,* 2002; Porter *et al.,* 1991). The feeding rate of many arthropod vectors increases at higher temperatures, thus increasing exposure of crops to mycotoxigenic fungi thereby increasing the spread of mycotoxins (Bale *et al.,* 2002; Dowd, 1992).

Insect damage has been shown to be closely related to *Fusarium* or *Aspergillus* ear rots (Miller 2001; Munkvold and Hellmich 2000). A field survey in Austria demonstrated that the incidence of the European maize borer increased *F. verticillioides* disease and fumonisin concentrations but not *F. graminierum* (Lew *et al.,* 1991). Therefore, the increased global warming and drought incidences will favor insect proliferation and herbivory, which will likely increase the incidence and severity of insect related damages as well as aflatoxin and fumonisin mycotoxins in maize. Higher average temperatures have the potential to change the geographical distribution of crops. This may in turn result in an expansion of the geographical distribution of insect-pests and their associated pathogens (e.g. maize streak virus, corn stunt complex that are vectored by different species of leaf hoppers), resulting in a change in the geographical distribution of diseases.

3.3. Strategies for mitigating climate related effects of biotic stresses on maize yields

Breeding for disease and insect resistance requires an understanding of parasite biology and ecology, disease cycles and drivers influencing the evolution of plant-pathogen interactions, because unlike abiotic stresses, biotic stress resistance is influenced by genetic variability in the pest/pathogen

population. As a result of the evolving pest/pathogen populations and the changes in fitness favoring new pathotypes/biotypes, improving resistance to biotic stresses has been a long term focus of agricultural researchers. The long-term success of breeding for disease or insect-pest resistance will depend on a more in-depth and clear understanding of: (i) the nature of the pathogen/insect-pest, and diversity of virulence in the populations; (ii) the availability, diversity and type of genetic resistance; (iii) availability of suitable sites (hot spots), screening methodologies/protocols for generating adequate disease/insect-pest pressures and tracking resistance; (iv) selection environments and methodologies for rapidly generating multiple stress resistant inbred lines, and their use in hybrid or variety development.

Significant progress has been made over the decades in the identification of stable genetic resistance for major maize diseases (Dowswell *et al.,* 1996; Bosque-Perez, 2000; McDonald and Nicol 2005; Pratt and Gordon, 2006; Welz and Geiger, 2000). However, the population structure of most maize pathogens remains inadequately characterized. Also, concerted efforts are required to widely test the available sources of resistance in multiple and relevant environments to expose them to a wide spectrum of pathogen strains and to facilitate identification of the most suitable resistance genes/alleles for use in the breeding programs. Research at CIMMYT is focused on multi-location phenotyping of a common set of 500 maize inbred lines for some prioritized diseases, namely GLS (gray leaf spot), TLB (turcicum leaf blight)(MSV (maize streak virus), and ear rots, across more than 15 locations in Sub-Saharan Africa, Latin America and Asia. This will help identify stable sources of resistance to key diseases and identify key phenotyping sites for future research. Using a common set of genotypes across environments will also provide the ability to monitor and detect emergence of new pathogen strains that will be registered as shifts in disease pressure and emerging new diseases, and how the environmental characteristics impacts pest biology and prevalence. CIMMYT has also developed several insect-pest resistant populations, inbred lines, and varieties, especially for the stem borers and post-harvest insect pests (weevils and grain borers) through projects such as Insect Resistant Maize for Africa (IRMA). In addition, several inbred lines have been developed combining resistance to stem borers and storage pests and these are currently being tested in eastern Africa. Wide testing of these materials in Kenya, Tanzania and Uganda is being done under IRMA.

3.4. Breeding approaches for tolerance to climate-related stresses

3.4.1. Conventional breeding

To increase the efficiency of breeding pipelines, a combination of conventional, molecular and transgenic breeding approaches will be needed. Breeding approaches are not mutually exclusive and are complimentary under most breeding schemes (Ribaut *et al.,* 201). Historically large gains have been made through conventional breeding. The success of the green revolution was based on breeding and resulted in large increases in cereal production (Evenson and Gollin, 2003). During the period of 1982 to 1994, the yield growth rate as a result of conventional breeding was 1.2 % worldwide (Duvick and Cassman, 1999). In temperate maize, breeding based on multi-location trials under different weather conditions has resulted in increased grain yields at a rate of 73 kg^{-1} ha^{-1} yr^{-1} under mild stress (Duvick, 1997). In tropical maize, conventional breeding has resulted in gains of up to 144 kg ha^{-1} yr^{-1} under drought stress (Edmeades et al. 1999). However, in the face of climate change, it is essential that

breeding pipelines are improved to meet the needs of future generations. In conventional drought breeding, the application of proven breeding methodologies in managed stress screening has been attributed to the significant gains in grain yield under drought stress (Bänziger et al. 2006). Up scaling training and application of these methodologies across projected drought prone environments will play a key role in the continued development of drought adapted maize. A similar approach will be required for additional abiotic and biotic stress expected to increase under future climates.

A vast amount of research has focused on individual stresses. However, in the farmers' fields the maize plants are regularly subjected to a combination of stresses. Relatively little is known about the physiological and molecular responses of crop plants subjected to stress combinations (e.g., drought + heat or drought + waterlogging); therefore, understanding the effects of different individual stresses as well as their combinations is an important step forward (Voesenik *et al.,* 2008). Breeding programs often run independent screens for stresses know to occur in the target environment, selecting genotypes which perform well across a suite of stresses. Independently screening for drought and low N tolerance in tropical maize identified several physiological traits associated with tolerance under one stress, conferred tolerance for the other stress (Bänziger *et al.,* 2000). Concurrent screening for both stresses successfully developed superior germplasm with tolerance to both stresses (Bänziger *et al.,* 2006). However, multiple stresses can have very different results and cannot be predicted from the combination of individual stresses (Mittler, 2006). Rizhsky *et al.,* (2004) exposed the model specie *Arabidopsis* to heat and drought stress simultaneously, and found that less than 10% of the regulated genes under combined heat and drought stress overlapped with the genes regulated by the individual stress treatments. These findings implied that the gene networks that control different stress combinations cannot be reliably predicted from those identified under specific individual stresses. Predicted climate change scenarios are likely to result in an increase in the stresses that plants face in the field. Given that combined tolerance to multiple stresses may be different to individual tolerance, research needs to focus on stress combinations likely to occur in the target environment. This will be particularly pertinent for drought stress and insect pests combined, drought and heat stress combined, and drought and waterlogging stress combined.

In the last 10 years, several institutions, especially in the private sector, have focused on the application of doubled haploid (DH) technology in breeding programmes, with an estimated 80 % of companies employing this technology (Röber *et al.,* 2005; Phillips, 2009). A doubled haploid is a genotype formed when haploid cells undergo chromosome doubling, allowing the production of a homozygous line after a single round of recombination. Blakeslee *et al.,* (1922) reported the production of the first haploid plant, and the first haploid maize was reported ten years later (Randolph, 1932). The use of DH technology in breeding has the potential to increase the efficiency of line development by reducing the time taken to reach homozygosity in conventional breeding technology from approximately six seasons to one season (Mohan Jain *et al.,* 1995). Initially the efficiency of chromosome doubling methods were too low for application within the maize breeding programmes; however, Röber *et al.,* (2005) developed a temperate inducer maize line called RWS with a relatively high induction rate (8.1%), thereby increasing the efficiency of DH development. Tropically adapted maize inducer lines with an induction rate of 10% are under development by CIMMYT, in collaboration with the University of

Hohenheim (Prigge *et al.,* 2011). The ability to apply DH technology within the tropical maize breeding could significantly improve the genetic gains in the breeding programmes. Work is currently underway to transfer this technology to the African breeding programs under the Bill and Melinda Gates Foundation funded project "Drought Tolerant Maize for Africa".

Genetic diversity is an essential component of breeding progress; however, to date, only a fraction of the available maize genetic diversity has been utilized by the plant breeders. Over 25,000 landraces, besides the wild relatives teosinte and*Tripsacum*, 3,000 elite inbreds, pools, and populations, are preserved in the CIMMYT Gene Bank (Ortiz *et al.,* 2009). Within the gene pool of maize's wild relatives, vast unexploited genetic diversity for novel traits and alleles exists that could be used to broaden the genetic base of breeding and deliver beneficial genetic variation (Ortiz *et al.,* 2009). Intensive selection may have resulted in reduced genetic diversity for specific traits, either directly or indirectly. Leveraging the hidden diversity within maize gene banks will potentially provide novel sources of favorable alleles to complement the ongoing breeding strategies. While the landraces are not generally used directly by the plant breeders because of their poor agronomic characteristics, however they can serve as sources of new inbred lines or DH lines from which new traits can be introduced into elite germplasm (Lafitte *et al.,* 1997). Simultaneously with the wider adoption of high throughput molecular tools, there is a distinct need to establish global phenotyping network for comprehensive and efficient characterization of genetic resources and breeding materials for an array of target traits, particularly for biotic and abiotic stress tolerance and nutritional quality. This would significantly accelerate genomics-assisted breeding, diversification of the genetic base of elite breeding materials, creation of novel varieties and countering the effects of global climate changes. A new initiative coordinated by CIMMYT in collaboration with many Mexican institutions, titled the *'Seeds of Discovery' (SeeD)*, aims to discover the extent of allelic variation in the genetic resources of maize and wheat, formulate core sets based on genotyping and phenotyping, and utilize marker-assisted breeding to bring those rare useful alleles into breeding programmes for developing novel genotypes.

3.4.2. Molecular breeding

The ability to quickly develop germplasm combining tolerance to several complex polygenic inherited abiotic and biotic stresses will be critical to the resilience of cropping systems in the face of climate change. Conventional breeding methods that rely on extensive phenotypic screening are effective but slow in producing germplasm tolerant to the current range of climatic conditions, and are not optimal for rapidly improving tolerance to multiple stresses. Molecular breeding offers the ability to increase the speed and efficiency of plant breeding (Whitford *et al.,* 2010). Molecular breeding is a general term used to describe modern breeding strategies where DNA markers are used as a substitute for phenotypic selection to accelerate the release of improved germplasm. Currently, the main molecular breeding schemes are marker assisted selection (MAS), marker assisted backcrossing (MABC), marker assisted recurrent selection (MARS) and genome-wide selection (GWS), as described in Table 3 (Ribaut *et al.,* 2010). Molecular marker-assisted breeding relies on the identification of DNA markers that have significant association with expression of specific target traits. The use of molecular techniques within breeding pipelines is widely, and successfully, employed within the private sector (Eathington *et al.,* 2007) and with greater emphasis in the public sector (Dwivedi *et al.,* 2007; Whitford *et al.,* 2010). The

development and availability of an array of molecular markers, greater throughput and reduced cost of genotyping assays, and above all, the recent availability of the complete maize sequence within the public domain (Schnable *et al.,* 2009) make the use of genotypic markers more accessible within the public sector breeding programs. Together these tools will allow key traits controlled by major genes as well as quantitative trait loci (QTL) to be more efficiently introduced into breeding pipelines.

The application of molecular breeding requires identification of genomic regions associated with the trait of interest. Molecular markers, and more recently high throughput genome sequencing, provide the ability to characterize genetic diversity within the germplasm pool for most crop species (Moose and Mumm, 2008). Since the development of DNA marker technology in the 1980s, great advances have been made in marker development, genetic maps, utilization of genome sequencing and the scale and cost of application of technologies (Dwivedi *et al.,* 2007). QTL mapping has been conducted for a wide range of traits, and extensive reviews have been published on yield (Holland, 2009), biotic stresses (e.g., Balint-Kurti and Johal, 2009; Wisser *et al.,* 2006; McMullen *et al.,* 2009), abiotic stresses (e.g., Salvi and Tuberosa 2005; Collins *et al.,* 2008;, Wassom *et al.,* 2008) and domestication related traits (e.g., Doebley, 2006). Initial results suggested plant populations generally segregate for a limited set of small effect QTLs with very few large effect QTLs (Salvi and Tuberosa, 2005) and QTLs were not consistent across mapping populations. Keys factors likely to be responsible for these results are genetic heterogeneity and small mapping population sizes, resulting in skewed distributions of QTL effects (Beavis, 1998; Holland, 2007). However, several studies have now been published using large population sizes for complex traits such as yield; while a large number of small effect QTLs were identified, together they accounted for less than half of the total genetic variation (Schon *et al.,* 2004). In general, a large number of small effect QTLs in maize have been identified for yield and abiotic stresses, while for many biotic stresses a few moderate to large effect QTLs have been identified.

The identification of genomic regions associated with tolerance to drought stress has been the subject of much research in maize (Ribaut *et al.,* 2009) and other crops (for reviews see Price and Courtois, 1999, Fleuery *et al.,* 2010). Drought studies have focused on the identification of the genetic basis of yield, yield components and secondary traits including increased flowering synchrony (ASI), root architecture, growth maintenance and stay green (see a review by Ribaut *et al.,* 2009). A large QTL mapping study to identify stable genomic regions associated with yield, yield components, and flowering parameters identified over 1080 QTLs (Ribaut *et al.,* 2009). Five QTL alleles for short ASI were introgressed through MABC from a drought-tolerant donor to an elite, drought-susceptible line. Under severe drought, the selected lines clearly outyielded the unselected control. However, their yield advantage decreased under mild to moderate drought stress (Ribaut and Ragot, 2007). As suggested by Collins *et al.,* (2008), the maintenance of biomass accumulation under water deficit should be considered as an optimization process between transpiration, biomass accumulation, and its partitioning between root and shoot, rather than as a tolerance process per se, and hence a given QTL can have positive, null, or negative additive effects depending on the drought scenario. This may have considerably slowed the utilization of QTL data for breeding. Relatively less research has been conducted on the identification of QTL associated with other abiotic stresses in maize, particularly for

heat stress. Frova and Sari-Gorla (1994) identified QTLs associated with pollen tolerance to a 2-hour heat stress of 50 °C during *in vitro* germination. Using a population of 45 maize RILs, five QTLs associated with high temperature germination and six QTLS for pollen tube growth were identified. Very few overlapping regions for both traits were identified, implying thats traits were independently regulated. Additionally no overlap was detected for QTLs under elevated and optimal temperatures. A later study by Frova *et al.,* (1998) using two maize mapping populations subjected to a heat stress (no information in terms of temperature and duration was provided) identified several QTLs associated with cell membrane stability, pollen germination and pollen tube growth. Using a larger mapping population in field conditions, a QTL accounting for 17 % of phenotypic variation in grain yield under heat stress and 28 % of the phenotypic variation in canopy temperature on chromosome 4A was recently identified in wheat (Pinto *et al.,* 2010). In case of waterlogging tolerance in maize, several moderate effect QTLs have been identified for seedling stage tolerance to waterlogging (Qui *et al.,* 2007). The authors screened a mapping population comprised on 288 $F_{2:3}$ lines derived from a cross between tolerance (HZ32) and sensitive (K12) inbred lines under flooded (6 cm above the soil surface for 6 days) and non-flooded conditions in a series of pot experiments. A total of 25 and 34 QTLs were identified in each experiment, accounting for between 4 to 37 % of the genotypic variation in tolerance to flooding. Moderate effect QTLs associated with shoot and root dry weight, total dry weight, plant height, and a coefficient of tolerance for water tolerance were identified across experiments on chromosomes 4 and 9. Mano *et al.,* (2005) developed an F_2 mapping population between a maize inbred line (B64) and teosinte (*Z. mays ssp. Huehuetenangensis*). The mapping population was grown in a pot experiment and flooded conditions were imposed for a period of 2 weeks. QTLs associated with adventitious root formation under flooding condition were identified on chromosomes 3, 7 and 8, Teosinte alleles contributed positively to all QTL confirming the potential use of *Z. mays* ssp*. Huehuetenangensis* as a donor within breeding programs targeting waterlogging tolerance. A similar study using a different teosinte accession (*Z. mays spp. Nicaraguensis*) crossed to maize inbred line B73 identified QTLs controlling constitutive aerenchyma formation on chromosomes 1, 5 and 8 (Mano *et al.,* 2009). The production of NILs containing these QTLs from the donor *Z. mays spp. nicaraguensis* is underway and providing a value genetic resource to confirm the potential of adventitious roots with aerenchyma to improved tolerance of maize to flooding.

QTLs conferring resistance to major maize diseases (TLB, downy mildews, SLB, rust, GLS, and many other diseases) and insect-pests have also been identified (Krakowsky *et al.,* 2004; Wisser *et al.,* 2006; Balint-Kurti and Johal, 2009; Garcia-Lara *et al.,* 2009). The first disease resistance QTLs to be cloned in maize, *Rcg1*, for resistance to anthracnose stalk rot was shown to be a Resistance Gene Analog (RGA) (Wolters *et al.,* 2006). A number of mapping studies have been undertaken for all the major diseases affecting maize (see reviews by Wisser *et al.,* 2006; Balint-Kurti and Johal 2009; Prasanna *et al.,* 2010). The disease QTLs mapping studies conducted thus far have provided information on the genetic architecture of disease resistance, including the number, location, and action of chromosomal segments conditioning the trait. Wisser *et al.,* (2006) further showed that QTLs for resistance to different diseases often clustered together, mirroring the clustered distribution of R genes and RGAs in plants. A similar concept was proposed by McMullen and Simcox (1995) for disease and insect resistance related

chromosomal regions in the maize genome. There is a clear need for further genetic dissection of these QTLs rich chromosomal regions to more precisely localize the genes involved by developing QTL-NILs.

The ultimate objective of QTL mapping is to identify the causal genes, or even the causal sequence changes, known as quantitative trait nucleotides (QTN) (Holland, 2007). Initial QTL mapping only provides an approximate localization to around 10-20cM. QTN identification requires a finer mapping in a high resolution, detailed genetic complementation studies and analyses of cosegregating sequence variants. Fine mapping can be done by selecting rare recombinants in the region of interest from very large populations that are nearly isogenic outside of the targeted region (Peleman *et al.,* 2005). With the large amounts of information available in public databases like the whole genome sequence of B73 (www.maizesequence.org), and HapMapSNPs, maize is in an ideal setting for such fine-scale studies. At CIMMYT, work is currently underway for fine-mapping major QTLs implicated in resistance to maize streak virus, gray leaf spot and northern corn leaf blight (NCLB) or turcicum leaf blight (TLB).

Bernardo (2008) observed that when a large proportion of phenotypic variation is controlled by many QTLs of small effects, the 'find-and-introgress-QTL' approach has limited applicability due to overabundance of QTLs identified for any given agronomic trait and their inconsistent effects across genetic backgrounds and environments. Recurrent selection relies on the phenotypic selection of superior progeny which are subsequently crossed with each other in every possible way to produce an improved source population thereby increasing the frequency of favourable alleles within a population. With the rapid reduction in genotyping costs currently underway, new genomic selection technologies have become available that allow the breeding cycle to be greatly reduced, and that facilitate the inclusion of information on genetic effects for multiple stresses in selection decisions (Heffner *et al.,* 2009). Three marker-based selection approaches are being utilized (F_2 enrichment, marker assisted recurrent selection, and genome-wide selection), that aim at increasing desirable QTL allele frequencies in a population improvement context, either by utilizing the QTL information or without it, are increasingly gaining prominence.

Both the F_2 enrichment and marker assisted recurrent selection (MARS) (Bernardo 2008) approaches require prior QTL identification through standard mapping procedures in a suitable population and markers that are either linked to the QTLs or located within the QTLs. In F_2-enrichment, the individual F_2 plants are screened with informative markers and the unfavorable homozygotes are removed to ensure all the remaining plants are carriers of desirable alleles (Bonnet *et al.,* 2005; Wang *et al.,* 2007) either in homozygous or heterozygous conditions. This increases the probability of success of deriving a superior recombinant inbred with smaller populations. However the effectiveness of this approach is reduced by the fact that only one generation of marker-based selection is performed in a typical F_2 enrichment exercise, with an additional round in the latter stages also not being efficient. MARS relies on multiple rounds of marker based selections with each cycle consisting of selected selfed progenies of each marker-selected individual and recombining these progeny to form the next generation material, thereby overcoming the problems associated with F_2 enrichment strategies. F_2 enrichment can target up to 9 to 12 unlinked QTLs. MARS allows larger number of marker loci to be

targeted (up to 30), however the products of MARS (recombinant inbreds) may not be fixed for the favorable allele at all target loci (Bernardo, 2008)

Genome-wide selection (often referred to as genomic selection) offers an alternative approach where no prior information on QTLs is required, with selection based entirely on the prediction of performance (Meuwissen, 2001; Hamblin *et al.,* 2011). Genomic estimated breeding values (GEBVs) are calculated for each individual in the population by fitting all the polymorphic markers as random effects in a linear model and these are used for the basis of selection. Simulation studies using different numbers of QTLs (20, 40, and 100) and levels of heritability showed response to genome-wide selection was 18 to 43% higher than the corresponding responses using MARS (Bernardo and Yu, 2007). This suggests the potential of genome-wide selection for complex traits governed by a large number of small effect QTLs. Heffner *et al.* (2009) suggested rapid-cycle genomic selection for abiotic stresses could increase genetic gains in stress tolerance breeding by two to three fold. Genome-wide selection has the potential to bypass problems associated with the number of QTLs controlling a trait, the distribution of effects of QTL alleles, and epistatic effects due to genetic background (Bernardo and Yu, 2007), facilitating the inclusion of information on genetic effects for multiple stresses in selection decisions (Heffner *et al.,* 2009). New breeding and selection strategies like genome-wide selection rely on the availability of cheap, robust and reliable marker systems. Pilot projects on the implementation of rapid-cycling genomic selection using much higher marker densities are being initiated by CIMMYT on new platforms based on next generation sequencing technologies, with the ultimate aim of its routine application across the CIMMYT and NARS maize breeding programs in Sub-Saharan Africa, Latin America and Asia.

3.4.3. Precision and High Throughput Phenotyping

Breeding progress relies on genetic variability for the trait of interest (e.g. grain yield under drought stress), high selection intensity through screening a large number of genotypes and high broad-sense heritability for the trait of interest. Improved phenotyping platforms will provide the foundation for the success of conventional, molecular and transgenic breeding. Yield is a function of many processes throughout the plant cycle thus integrative traits that encompass crop performance over time or organization level (i.e. canopy level) will provide a better alternative to instantaneous measurements which only provide a snapshot of a given plant process (Araus *et al.,* 2008). Many new phenotyping tools based on remote sensing are now available including non-destructive measurements of growth-related parameters based on spectral reflectance (Marti *et al.,* 2007) and infrared thermometry to estimate plant water status (Jones *et al.,* 2009).

New phenotyping tools together with advances in molecular technologies will be a powerful combination towards rapid advances in germplasm improvement. However to ensure the full potential of such tools, greater emphasis needs to be given to reducing the within-experimental site variability. Fields experiments provide the cornerstone for all germplasm development; however, the importance of environmental uniformity and good agronomic practices are often overlooked. Without uniform phenotyping field sites the much anticipated benefits of molecular breeding will not be realized. Highly variable field sites will produce highly variable data, thereby masking important genetic variation for key

traits, regardless of the cost and precision of a specific phenotyping tool. Phenotypic variation among individuals could be due to genetic and environmental factors. Broad sense heritability estimates, therefore, reflect the amount of variation in genotypic effects compared to variation in environmental effects. Heritability is specific to a specific population within in a specific environment and can be reduced due to increased environmental variation without any genetic change occurring. Broad sense heritability (H) is defined as the proportion of ^{2} phenotypic variation that is due to genetic variation (Falconer and Mackay, 1996) and is defined as:

$$H = \frac{\sigma^2 G}{\sigma^2 G + \frac{\sigma^2 GE}{e} + \frac{\sigma^2 E}{re}}$$

where $\sigma^2 G$ is the genotypic variance and $\sigma^2 E$ is the phenotypic variance, *e* is the number of environments or locations and *r* is the number of reps, calculated from variance components obtained from an analysis of variance. Since phenotypic variation of a population is caused by both genetic (signal) and environmental factors (noise), broad sense heritability provides a useful estimate to determine the proportion of phenotypic variance that can be attributed to genetic effects. Broad sense heritability is population specific within a particular environment and typically decreases with increased site (environmental) variability. As a result, by identifying and implementing methods to reduce environmental variation within agricultural trials, broad sense heritability can be increased resulting in potentially greater selection gains.

Increasing trial heritabilities through reduced environmental error is therefore essential to improve the cost-effectiveness of phenotyping and increase the genetic progress in the development of climate-ready germplasm. This is particularly pertinent for breeding for abiotic stress tolerance, where variability can be masked under optimal conditions (Bänziger *et al.,* 2000). Soil variability is a major cause of inherent site variability. Additional generators of within-site variability include topography, bordering and crop management (Blum *et al.,* 2011). A recent review of field variability within rice drought phenotyping sites highlighted variability in soil physical properties within and between experimental sites (Cairns *et al.,* 2011). In general relatively little is known, and even less reported, about soil properties and variability within phenotyping. Initial characterization of field sites prior to use for phenotyping will allow researchers to exclude sites where large experimental error is likely to be introduced through highly variable soil properties. In phenotyping sites with moderate to high heterogeneity, variability maps of important characteristics for specific trials (e.g. soil texture for drought trials and residual nitrogen levels for low nitrogen trials) will allow researchers to avoid areas of high variability or design trials incorporating spatial variability. Experiments can be planted within areas of the least spatial variability and/or individual trials blocked within variability gradients to reduce within experiment or within replicate environmental error (Cairns *et al.,* 2004; Cairns *et al.,* 2009).

Site characterisation is often used for precision agriculture applications but is less frequently applied within public breeding programs. Many techniques are available for mapping variability within field sites based on soil sampling, soil sensors and measurements of plant growth as surrogates of

variability. Destructive soil sampling for key soil physical and chemical properties conducted on a grid sample can provide a low-cost measure of soil variability. Soil texture strongly influences water holding capacity, water release characteristics and nitrogen mineralization (Marshall *et al.,* 1996). Within site variability in soil texture can introduce variation in the development of drought stress as a result of the variation in water release characteristics. Electromagnetic (EM) surveys can be used as a surrogate for soil texture and salinity. Ground-based EM surveys have been used for many years to infer areas of saline soils (Cameron *et al.,* 1981), to delineate soil spatial variability (Johnson *et al.,* 2003) and as a surrogate for some soil characteristics such as soil moisture and clay percentage (Sudduth *et al.,* 2001). The most common instruments used for soil apparent electrical conductivity measurement are the EM38 and EM31 conductivity meters (from Geonics Ltd).

3.5. Crop management options for increasing the resilience of maize systems to climate-related stresses

The use of conventional farming practices based on extensive tillage, especially when combined with removal or *in situ* burning of crop residues, has accelerated erosion while the soil resource base has been steadily degraded (Montgomery, 2007). Despite the availability of improved crop varieties with increased yield potential, the optimum production is not attained generally because of poor crop management (Reynolds and Tuberosa, 2008). Cropping systems will thus have to be more robust and resilient to buffer extreme weather events, i.e. drought and flooding. New agricultural practices will not only have to prevent further soil degradation, but also improve the resilience of the system while reducing production costs. Conservation agriculture has been proposed as a set of management principles that assures a more sustainable agricultural production and reducing productions costs while increasing profitability. It combines reduced tillage, retention of adequate levels of crop residues maintaining soil surface cover and crop rotations. These conservation agriculture principles are applicable to a wide range of crop production systems, however, the application of conservation agriculture will vary with climate, biophysical soil characteristics, system management conditions and farmer circumstances. Specific and compatible management components (e.g. pest and weed control, nutrient management strategies, rotation crops, appropriately-scaled implements) will need to be identified through adaptive research with active farmer involvement.

Improved agronomic management can improve soil quality and make cropping systems more resilient to changing environmental conditions. Conservation agriculture, based on minimum tillage, crop residue retention and crop rotation, can improve infiltration and reduce evaporation compared to practices involving conventional tillage and zero tillage without retention of adequate levels of crop residue (Verhulst *et al.,* 2010). The reduction in tillage and increased carbon input in conservation agriculture result in more stable aggregates (Bronick and Lal, 2005). Residue cover prevents aggregate breakdown, and thus crust formation, which is caused by direct raindrop impact as well as by rapid wetting and drying of soils (Le Bissonnais, 1996). In addition, the residue cover slows down runoff, giving the water more time to infiltrate.

Crop residue retention at the soil surface reduces soil evaporation compared to bare soil (Hatfield *et al.,* 2001). The improved infiltration and reduced evaporation means that more water is

available for crops under conservation agriculture than for conventional tillage and zero tillage with residue removal. Mupangwa *et al.,* (2007) determined the effect of mulching and tillage on soil water content in a clayey and a sandy soil in Zimbabwe. Mulching helped conserve soil water during a season with long periods without rain at both experimental sites. Soil water content consistently increased with increase in surface cover across the three studied tillage practices (planting basins, ripper tine and conventional plough). Gicheru *et al.,* (1994) showed that crop residue mulching resulted in more moisture down the profile (0-120 cm) throughout two crop periods (the short rains and the long rains) over two years than conventional tillage and tied ridges in a semi-arid area of Kenya. Alvarez and Steinbach (2009) reviewed the results of experiments where plow tillage (mouldboard plow), reduced tillage (chisel plow, disk plow or disk harrow) and zero tillage were compared in the Argentine Pampas where soybean (*Glycine max*), maize (*Zea mays*) and wheat (*Triticum aestivum*) were the main crops. Soil water content was similar under plow and reduced tillage, whereas zero tillage with residue retention had a higher soil water content at planting and flowering than both systems with tillage. When soils were wet, differences between tillage systems were small but soil water content was higher for zero tillage with residue retention as conditions leading to soil drying occurred. Verhulst *et al.,* (2011) evaluated soil water content (0-60 cm) in different tillage and residue management practices in the semi-arid areas of the Mexican highlands for a maize-wheat rotation. Zero tillage with residue retention had higher soil water content than zero tillage with residue removal and conventional tillage with or without residue, and the effect was more pronounced in dry periods.

A higher soil water content in conservation agriculture can buffer for short drought periods during the growing season. Consequently, conservation agriculture may significantly improve crop yield in years of poor rainfall distribution, compared to practices involving conventional tillage or zero tillage without crop residue retention. This was confirmed in the semi-arid highlands of Mexico where maize yields were similar among tillage and residue management practices in years with good rainfall distribution. However, in a year with an extended drought period during the vegetative maize growth (30-83 days after planting) the yield for conservation agriculture practices was 1.8 to 2.7 times higher than for zero tillage with residue removal and conventional tillage with or without residue (Verhulst *et al.,* 2011). Also Thierfelder and Wall (2009) reported that, depending on the season, maize yields were equal or higher using conservation agriculture practices compared with conventional tillage in Zambia and Zimbabwe. Rockström *et al.,* (2009) found that reducing tillage in maize systems in Kenya, Tanzania and Zambia resulted in significantly higher rain water productivity and yield for most locations. Alvarez and Steinbach (2009) reported that maize yields were lower with zero or reduced tillage than with mouldboard tillage without nitrogen fertilizer, but yield differences disappeared when fertilizer was applied in the Argentine Pampas. The positive effect of mulching on soil water content reported by Mupangwa *et al.,* (2007) did not result in an increase in maize yields, since no significant effect of mulching on yield was found.

Excess water can be removed from the root zone by lowering the water tables with drainage. Waterlogging can also be minimized by management practices that improve infiltration such as conservation agriculture and planting systems that elevate the rooting zone above standing water such as raised bed planting. Cox *et al.,* (1990) found that maize grain yields were significantly higher under

bed planting than under conventional or zero tillage on the flat on an undrained soil that flooded periodically in the northeastern US (Fausey 1990) evaluated permanent raised beds for use on slowly permeable soils. Plant stands were more uniform over a range of improved drainage levels and maize grain yields were always highest with the bed or ridge system. Ogban and Babalola (2002) reported that green maize yield was higher for a mound-tillage system than for raised bed planting and zero tillage systems in three wet inland valley bottoms in southwestern Nigeria.

4. Mitigation technologies and practices for reducing greenhouse gas emissions and enhancing carbon-storages

4.1. Nitrogen use efficiency

An important mitigation strategy for climate change is a reduction on the reliance of chemical inputs while maintaining yields. Nitrogen fertilization is one of the most important inputs for maize production in many regions of Asia, and North and South America, and represents a significant production cost for the farmer. The price of nitrogen has quadrupled since 2000 (Piesse and Thirtle, 2009), and in the US, the recent rise in the fertilizer prices is estimated to have increased production costs by 15% (Mitchell, 2008). In the past 40 years N fertilizer consumption has steadily increased, for example Latin America has seen an eleven-fold increase in N fertilizer consumption (Ladha *et al.,* 2005), with total N fertilizer consumption in Central and South America reaching 1.31 and 8.41 M t (FAOSTAT, 2008). In contrast, nitrogen use efficiency has steadily declined, with cereal crop production per unit of applied N decreasing (Dobermann and Cassman, 2005). Generally more than 50 % of applied N is not assimilated by plants. The environmental impacts of increased nitrogen use through nitrate leaching, the use of fossil fuels to manufacture, transport and apply fertilizers, and N_2O emissions associated with denitrification are high (Foulkes *et al.,* 2009). Globally, N fertilizers account for 33 % of the total annual creation of reactive nitrogen (Nr) and 66 % of all anthropogenic sources of reactive forms of Nr (Dobermann and Cassman, 2005). Nr contributes to air pollution and the greenhouse effect. In view of the environmental costs of producing, transporting and using synthetic nitrogen fertilizers, there is growing interest in identifying methods to reduce or optimize nitrogen application in agriculture and to develop crop varieties that are more responsive to nitrogen application (Vitousek *et al.,* 1997).

In sharp contrast to the rest of the world, fertilizer application in sub-Saharan Africa is negligible. Barely 1 % of global nitrogen fertilizer application occurs in sub-Saharan Africa although the region accounts for 13 % of global cultivated land (Leff *et al.,* 2004). Average fertilizer application (including P and K) in Sub Saharan Africa is 9 kg ha^{-1} compared to 100 kg ha^{-1} in South Asia, 73 kg ha^{-1} in Latin America and over 250 kg ha^{-1} in Western Europe and North America (Molden, 2007). Reasons for poor adoption of fertilizers by African farmers include high costs and poor infrastructure. African farmers are amongst the poorest in the world, yet fertilizer prices are two to six times the world average (Pinstrup-Andersen *et al.,* 1999). Cereal yields in sub-Saharan Africa have remained stagnant at just over 1 t ha^{-1} since 1960. During this period, the population has almost quadrupled resulting in increased demand for food, which has largely been met by expanding production into forested areas and marginal lands (UN, 2008). In East Africa, where maize is the staple food, average maize yields increased marginally from 1.0 t ha^{-1} in 1961 to 1.3 t ha^{-1} in 2009. During the same period, land under maize cultivation rose from 5.6 million ha to 14.1 million ha (equivalent to 50% of the land currently used for maize cultivation in

America). Deforestation accounts for 1.5 billion tons of carbon release annually into the atmosphere which accounts for almost 20 % of carbon emission due to human activity (Canadell, 2007). The clearing (burning) of forested land in tropical regions for agricultural use is one of the primary sources of greenhouse gas emissions. Reducing or preventing deforestation would have the largest and most immediate impact on reducing atmospheric carbon emissions (IPCC 2007). Maintaining carbon sinks in tropical forests is therefore one of the major climate change mitigation measures. Poor intensification of agriculture in sub-Saharan Africa (low use of fertilizer and irrigation) has resulted in a large expansion of agricultural land within this region (FAO 1997; 2003). It is estimated that since 1980, 58% of new agricultural land in Africa was developed through deforestation (Brink and Eva, 2008). Between 1980 and 2000, agricultural land in all developing countries increased by 629 million hectares, largely at the expense of forests (Gibbs *et al.,* 2010). In the developing world, cultivated land is expected to increase by 47 % by 2050 of which over two-thirds will be developed as a result of deforestation and wetland conversion (Fischer and Heilig, 1997). In order to prevent large scale deforestation and expansion of agricultural land, intensification of agricultural systems is likely to be the most sustainable method to meet food demand (Cassman *et al.,* 2003). The development of crop varieties with improved NUE under low input conditions is, therefore, likely to have a major impact not only on livelihoods and food security, but also in terms of climate change mitigation through preservation of forests.

NUE can be defined as the amount of grain produced per unit of available soil N (including fertilizers (Moll *et al.,* 1982). NUE can be separated into N-uptake efficiency (N uptake per unit available soil N and N-utilization efficiency (grain production per unit absorbed N) (Moll *et al.,* 1982). Improved agronomic management options and genetic enhancement both have the potential to increase NUE and N stress tolerance. Management options related to N rate, timing, source and placement can be used to optimize N uptake (Ortiz-Monasterio *et al.*, 2010). In sub-Saharan Africa where fertilizer use is minimal, genetic approaches to maintenance of yield levels at reduced rates of N application are crucial. Large genetic variation in NUE exists within the maize (Lafitte *et al.,* 1997; Bertin and Gallais, 2001; Gallais and Hirel, 2004; Gallais and Coque, 2005). Modern high-yielding maize germplasm has been selected under optimal N. Selection pressure in these environments may have reduced genetic variation for performance under low N conditions (Lafitte *et al.,* 1997). Thus, it may be important to exploit landraces within NUE breeding programs.

Despite large genetic variation for NUE, breeding for NUE in both low input and intensive agricultural systems remains challenging. NUE is controlled by many genes/QTLs with minor effects. Developing varieties with superior NUE or introgressing NUE traits into elite germplasm requires a long term breeding strategy. For breeding progress care must be taken to ensure reduce the high environmental noise often encountered within low N experimental trials, where sub-optimal fertilization exposes field variation in soil fertility as a result of variability in soil texture, organic matter and historical management practices and land use (Banziger and Lafitte, 1997). In addition to exploiting existing genetic variation, introduction of novel genes through genetic modification offers an additional, targeted approach to improving NUE in crop plants. Recent studies using transgenics have successfully increased NUE in canola (Good *et al.,* 2007) and rice (Bi *et al.,* 2009). Complementary to exploiting genetics for improved NUE, breeding programs need to establish field screening protocols particularly

where NUE is being targeted for sub-optimal levels of fertilization such as in Africa or parts of Europe and North America where farmers are being encouraged to reduce fertilizer application. Traditionally, crop trials, including those from which green revolution varieties were developed, have been conducted under well managed field station conditions with optimal nutrient application to reduce the effect of field variability. Most breeding programs worldwide continue to use this model despite the fact that farmers in many parts of the world, particularly developing tropical regions, rarely fertilize at optimal levels. To determine yield response at sub-optimal or low levels of fertilization, specific low N screening locations need to be established which expose genetic variation in NUE under conditions reflective of the target environment (Inthapanya *et al.,* 2000; Sahu *et al.,* 1997; Singh *et al.,* 1998). Direct selection under low N screening has been found to be more efficient than indirect selection under high N (Presterl *et al.,* 2003).

4.2. *Management practices to reduce the global warming potential of cropping systems*

Improved agronomic practices can help to mitigate global warming by reducing CO_2 emissions from cropping systems. The net global warming potential (GWP) of a cropping system is determined by CO_2 emissions associated with farming activities, soil C sequestration and emissions of greenhouse gases (GHG) from the soil (Robertson *et al.,* 2000). The development of sustainable management practices for individual components of GWP need to be evaluated.

4.2.1. CO_2 emissions associated with farming activities

To include farming activities estimates must be made of energy use and C emissions for primary fuels, electricity, fertilizers, lime, pesticides, irrigation, seed production, and farm machinery (West and Marland, 2002). Synchronizing nutrient supply with plant demand and using the appropriate rate, source and placement can increase nutrient use efficiency and reduce the amounts of fertilizer used in maize systems (Sitthaphanit *et al.,* 2009; Wang *et al.,* 2007; Ma *et al.,* 2004).

Conservation agriculture reduces the CO_2 emissions associated with farming activities by the reduction of tillage operations. West and Marland (2002) reported estimates for C emissions from agricultural machinery, averaged over maize, soybean and wheat crops in the USA at 69.0, 42.2, and 23.3 kg C ha^{-1} per year for conventional tillage, reduced tillage and zero tillage respectively. While enhanced C sequestration in soil can only continue for a finite time, the reduction in net CO_2 flux to the atmosphere, caused by reduced fossil-fuel use, can continue indefinitely, as long as the alternative practice is continued, and this could more than offset the amount of C sequestered in the soil in the long term (West and Marland, 2002). No reports have been found for the reduction of CO_2 emissions associated with a reduction of tillage operations in maize systems using animal traction or manual land preparation, but it can be assumed that the reductions in CO_2 emissions would be smaller.

The efficient use of irrigation water can also reduce CO_2 emissions. Irrigation contributes to CO_2 emissions because energy is used to pump irrigation water and, when dissolved, calcium (Ca) precipitated in the soil, forming $CaCO_3$ and releasing CO_2 to the atmosphere (Schlesinger, 2000). Optimizing irrigation management, i.e. irrigation scheduling and methods of application, can result in important irrigation water savings. Steele *et al.,* (2000) compared irrigation scheduling based on water

balance methods, CERES-Maize model estimates of plant extractable water or tensiometer and canopy temperature measurements in the northern Great Plains. They found that, compared to other commercial growers in the area, maize yields increased by 5% while irrigation inputs decreased by 30% with any of the four techniques. Hassanli *et al.,* (2009) compared subsurface drip, surface drip and furrow irrigation for maize in southern Iran and reported significant differences in irrigation water use efficiency which was the highest for subsurface drip (2.12 kg m^{-3}) and the lowest for furrow irrigation (1.43 kg m^{-3}). Conservation agriculture can also reduce the use of irrigation water by conserving more soil water or increasing irrigation efficiency due to the improved infiltration. Harman *et al.,* (1998) report the elimination of the pre-sowing irrigation in a zero tillage system, resulting in water savings of 25% compared to conventional tillage systems for maize and sorghum in the Texas High Plains.

Herbicide use has increased in the US maize production systems with the switch from conventional tillage with the moldboard plow to zero tillage (Lin *et al.,* 1995), but in the full C cycle analysis for USA farming systems, the increase in herbicide use was offset by far by the reduction in fossil fuel for tillage operations (West and Marland, 2002). Based on USA average crop inputs, zero tillage emitted less CO_2 from agricultural operations than did conventional tillage, with 137 and 168 kg C ha^{-1} per year respectively, including the C emissions associated with the manufacture, transportation, and application of fertilizers, agricultural lime, and seeds (West and Marland, 2002).

4.2.2. Soil C sequestration

Carbon levels in soil are determined by the balance of inputs, as crop residues and organic amendments, and C losses through organic matter decomposition. Management to build up SOC requires increasing the C input, decreasing decomposition, or both (Paustian *et al.,* 1997). The C input may be increased by intensifying crop rotations, including perennial forages and reducing bare fallow, by retaining crop residues, and by optimizing agronomic inputs such as fertilizer, irrigation, pesticides and liming. Decomposition may be slowed by altering tillage practices or including crops with slowly decomposing residue in the rotation. In order to understand better the influence of different management practices with special emphasis on tillage, crop rotation and residue management, on C sequestration, Govaerts *et al.,* (2009) did an extensive literature review. They concluded that in general, information was lacking on the influence of tillage and crop rotation on C stocks for the developing world and the more tropical and subtropical areas.

On the effect of tillage practice on soil C stocks, most studies report that organic matter increases in the topsoil, mainly in the 0-5 cm soil layer, for zero tillage compared to conventional tillage when residues are retained (Feller and Beare, 1997; Six *et al.,* 1999; Sainju *et al.,* 2006). Zero tillage favors the formation of stable aggregates that physically protect organic matter thereby reducing mineralization rates (Lichter *et al.,* 2008). Tillage breaks up soil aggregates so that organic matter becomes available for decomposition (Six *et al.,* 2000; Bronick and Lal, 2005). Tillage reduces C in the topsoil layers, but might increase it in the deeper soil layers as organic material is moved downwards and mixed in the plow layer (VandenBygaart and Angers 2006). Therefore this review and that of Govaerts *et al.,* (2009) only consider results from measurements done to at least 30 cm deep after at least 5 years of continuous practice. For maize systems, Govaerts *et al.,* (2009) found 48 reported

comparisons of C stocks in zero tillage versus conventional tillage, of which the majority (41 comparisons) were carried out in North America. For 19 comparisons, an increase in soil C stocks was reported for zero tillage over conventional tillage. For 18 comparisons, no significant differences were found and for 5 comparisons, a negative effect of zero tillage on C stocks was reported (Govaerts *et al.,* 2009). Mishra et al. (2010) reported that on one farm in the Corn Belt of Ohio, the soil organic C stock in the top 40 cm was significantly greater under zero tillage than conventional tillage in three long-term experiments, but no significant differences were found on two other farms. Dong *et al.,* (2009) studied the effect of tillage and residue management on soil C stocks in a loam soil cropped in a winter wheat–corn rotation in northern China. For total C stock, the management practices were in the order: zero tillage with chopped residue > rotary tillage with chopped residue > moldboard tillage with chopped residue > moldboard tillage without residue > zero tillage with whole residue.

Altering crop rotation can influence soil C stocks by changing the quantity and quality of organic matter input. Increasing rotation complexity and cropping intensity is expected to increase the soil organic C stocks. In the literature review by Govaerts *et al.,* (2009), crop diversification increased the soil C stock in 14 of the 26 withheld comparisons in maize systems, but it did not have a significant effect on three comparisons and decreased C stock in the remaining nine.

The increased input of C as a result of the increased productivity due to crop intensification will result in increased C sequestration. VandenBygaart *et al.,* (2003) reported in their review of Canadian studies that, regardless of tillage treatment, more frequent fallowing resulted in a lower potential to gain SOC in Canada. Also eliminating fallows by including cover crops promotes SOC sequestration by increasing the input of plant residues and providing a vegetation cover during critical periods (Franzluebbers *et al.,* 1994; Bowman *et al.,* 1999), but the increase in SOC concentration can be negated when the cover crop is incorporated into the soil (Bayer *et al.,* 2000). Forage crops could accumulate more C in soils, compared to grain crops, due to a higher root biomass production stimulated by grazing or mowing. Dos Santos *et al.,* (2011) determined the contributions of cover crop- or forage-based zero tillage rotations and their related shoot and root additions to the C stocks of a subtropical Ferralsol. Forages or legume cover crops contributed to C sequestration and most of this contribution came from roots. Crop residue mass may not be the only factor in SOC retention by agricultural soil. The mechanism of capturing C in stable and long-term forms might also be different for different crop species (Gál *et al.,* 2007).

4.2.3. Trace gas emissions

The potential to offset greenhouse gas emissions from energy and industrial sources is largely based on studies documenting the CO_2 mitigation potential of conservation agriculture. It is important, however, to consider the net result of fluxes for all three major biogenic greenhouse gases (i.e. CO_2, N_2O and CH_4) on radiative forcing, which is essential for understanding agriculture's impact on the net global warming potential. Soil management practices are known to affect the CO_2, CH_4 and N_2O (Ball *et al.,* 1999; Omonode *et al.,* 2007).

Emission of CO_2 is often lower in zero tillage than in conventional tillage (Sainju *et al.,* 2008; Almaraz *et al.,* 2009) although the opposite has also been reported (Oorts *et al.,* 2007). Johnson *et al.,* (2010) found that CO_2 flux increased briefly after tillage in the Northern Corn Belt of the USA, but the effect of tillage was negligible when the CO_2 flux was integrated across an entire year. Although fertilizer applications are the largest contributors to N_2O emission from soil, tillage can increase emission of N_2O in maize systems (Beheydt *et al.,* 2008; Ussiri *et al.,* 2009), have no effect (Jantalia *et al.,* 2008; Johnson *et al.,* 2010) or decrease emission of N_2O compared to zero tillage (Robertson *et al.,* 2000). Emission of N_2O is the result of so many interacting processes that it is difficult to predict how tillage practice will affect it. It can be assumed that lower temperatures, better soil structure and less compact soils in zero tillage than in conventional tillage will reduce emissions of N_2O, while increased soil organic matter, water content and mineral N contents will favor emissions of N_2O.

Soils can be a net sink or source of CH_4, depending on different factors, such as water content, N level, organic material application and type of soil (Gregorich *et al.,* 2005; Liebig *et al.,* 2005). Methane is consumed by soil methanotrophes, which are ubiquitous in many soils (McLain and Martens, 2006), and is produced by methanogenic microorganisms in anaerobic soil locations (Chan and Parkin, 2001). Agricultural systems are usually not a large source or sink of CH_4 (Chan and Parkin 2001; Johnson *et al.,* 2010; Bavin *et al.,* 2009) but soil as a sink for CH_4 is far less important than as a source of N_2O.

5. Conclusions

Farmers have a long record of adapting to the impacts of climate variability. However, based on current scientific knowledge, the probably impacts of climate change are out of the range of farmers' previous experiences and represent a greater challenge. Climate change will, hence, severely test the farmers' resourcefulness (Adger *et al.,* 2007). This review focused on technologies for the development of improved germplasm, however this is only the first step in the process. Adaptation to climate change requires cross-disciplinary solutions (Howden *et al.,* 2007) that include the development of appropriate germplasm and mechanisms to facilitate farmers' access to the germplasm. Seed production and deployment, effective policies and management strategies at the country, regional and international levels will all be required to ensure the technologies reach the intended beneficiaries and make the desired impacts.

Varieties with increased resilience abiotic and biotic stresses will play an important role in autonomous adaptation to climate change (Easterling *et al.,* 2007; Fedoroff *et al.,* 2010). Over fifty years ago scientists were able to offset yield losses by up to 40% through the development of improved germplasm and management options (Eveson and Gollin, 2003). Today scientists are faced with an even harder challenge – to meet the needs of future generations in the face of both population growth and climate change. While this challenge is immense, the advancement in molecular and phenotyping tools combined with the vast accumulated knowledge on mechanisms responsible for yield loss will provide a solid foundation to achieve increases in productivity within maize systems.

Acknowledgements

This work was supported by the Drought Tolerance Maize for Africa (DTMA) project, funded by the Bill and Melinda Gates Foundation. N. Verhulst received a PhD fellowship of the Research Foundation - Flanders. The boundaries and names shown and the designations used on all maps do not imply official endorsement or acceptance by the authors.

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Table 1. Population size, total maize area, calorie intake due to maize consumption and average maize yields in sub-Saharan Africa.

	Population (thousands)[a]				% of total calorie intake from maize consumption[b]	Maize yield[b] (t ha^{-1})				
Country	1950	2009	2050	Total area[b] (ha)		1961 - 1970	1971-1980	1981-1990	1991-2000	2001-2008
North Africa										
Sudan	9,190	42,272	75,884	3,0672	1.8	0.64	0.67	0.50	0.58	1.17
West Africa										
Benin	2,050	8,935	21,982	746,318	19.8	0.56	0.69	0.78	1.09	1.17
Burkina Faso	4,080	15,757	40,830	608,368	14.9	0.63	0.77	0.90	1.52	1.62
Cape Verde	146	506	703	34,385	12.5	0.52	0.36	0.44	0.40	0.30
Cote d'Ivoire	2,505	21,075	43,373	310,000	7.5	0.76	0.61	0.74	0.80	0.81
Ghana	4,981	23,837	45,213	750,000	2.4	1.09	1.05	1.05	1.47	1.54
Guinea	2,619	10,069	23,975	484,296	13.9	1.08	1.10	1.06	1.23	1.57
Guinea-Bissau	518	1,611	3,555	17,000	3.5	0.71	0.68	0.83	0.99	1.64
Gambia	258	1,705	36,763	43,460	10.0	0.69	1.17	1.42	1.39	1.17
Mali	4,268	13,010	28,260	329,023	9.1	0.86	1.11	1.26	1.36	1.49
Mauritania	651	3,291	6,061	20,000	1.1	0.66	0.48	0.57	0.78	0.76
Niger	2,462	15,290	58,216	10,476	1.2	0.64	0.66	0.54	0.73	0.81
Nigeria	36,680	154,729	289,083	3,845,000	7.6	0.89	1.05	1.31	1.28	1.64
Senegal	2,416	12,534	26,102	227,741	12.6	0.80	0.85	1.17	1.05	1.8
Togo	1,329	6,619	13,196	487,175	22.3	0.61	1.09	0.89	1.01	1.20
Central Africa										
Angola	4,148	18,498	42,267	1,115,000	18.2	0.83	0.68	0.37	0.49	0.63
Cameroon	4,466	19,522	36,736	480,000	13.7	0.80	0.89	1.61	1.81	2.02
Central African Republic	1,327	4,422	7,603	130,000	12.4	0.69	0.47	0.76	0.92	0.93
Chad	2,429	11,206	27,776	235,082	5.4	1.19	1.48	0.85	0.99	0.89

Congo	808	3,683	6,863	10,250	2.2	0.76	0.61	0.74	0.80	0.81
Democratic Republic of Congo	12,184	66,020	147,512	1,483,890	12.6	0.70	0.60	0.77	1.19	2.2
Eastern Africa										
Burundi	2,456	8,303	14,846	115,000	12.2	1.03	1.14	1.22	1.26	1.07
Eritrea	1,141	5,073	10,787	17,000	1.7	-	-	-	0.49	0.56
Ethiopia	18,434	82,825	173,811	1,767,389	18.2	-	-	-	1.57	1.94
Kenya	6,077	39,802	85,410	1,700,000	35.2	1.22	1.37	1.78	1.65	1.67
Madagascar	4,084	19,625	42,698	250,000	6.3	1.11	1.03	1.07	0.91	1.40
Malawi	2,882	15,263	36,575	1,596,955	52.8	1.03	1.17	1.13	1.29	1.39
Mozambique	6,442	22,894	44,148	1,400,000	22.7	0.95	0.72	0.41	0.72	0.86
Rwanda	2,162	9,998	22,082	110,000	5.6	1.19	1.07	1.27	1.14	0.811
Tanzania, United Republic of	7,560	43,739	109,458	3,100,000	34.1	0.49	1.42	1.33	1.63	1.07
Uganda	5,158	32,710	91,271	862,000	9.2	1.11	1.30	1.27	1.51	1.61
Zambia	2,340	12,935	28,857	663,990	50.7	0.83	1.37	1.88	1.59	1.78
Southern Africa										
Botswana	412	1,950	2,758	56,000	19.9	0.41	0.54	0.356	0.27	0.23
Lesotho	734	2,067	2,491	160,000	53.3	0.74	0.89	0.82	0.89	0.65
Namibia	485	2,171	3,588	18,000	16.0	1.20	1.23	1.14	0.86	1.71
South Africa	13,683	50,110	56,802	2,799,000	30.0	1.32	1.92	1.90	2.20	3.17
Swaziland	273	1,185	1,749	47,409	23.5	0.49	1.42	1.33	1.63	1.07
Zimbabwe	2,747	12,523	22,178	1,730,000	42.4	1.25	1.73	1.51	1.25	0.74

[a]Data from the World Populations Prospects, 2008 Revision using medium variant (United Nations, 2009)

[b]Data from FAOSTAT (2010)

Table 2. Major biotic stresses associated with maize production losses in Asia, Africa and Latin America.

Ecological environment	Highland/Transitional	Mid-altitude/Subtropical	Tropical Lowland
East and South East Asia	Branded leaf and sheath blight	Downey mildew	
	Borers (*Chilo* spp)	Borer (*Chilo, Sesamia* spp.)	
South Asia	Turcicum blight	Turcicum blight	Downy mildew
		Borers (*Chilo, Sesamia* spp.)	Borers (*Chilo, Sesamia* spp.)
Sub-Saharan Africa	Turcicum blight	Gray leaf spot	Striga
	Common rust	Streak virus	Streak virus
	Ear rots	Ear rots	Borers
		Weevils	
		Borers (*Chilo, Sesamia* spp.)	
Latin America and Caribbean	Ear rots	Turcicum blight	Fall armyworm
	Rust	Borer (S. W. corn borer)	Corn stunt complex
	Turcicum blight	Tar spot complex	Ear rots
		Ear rots	Gray leaf spot
		Gray leaf spot	

Table 3. Current molecular breeding strategies (adapted from Ribaut *et al.,* (2010))

Strategy	Description
Marker assisted selection (MAS)	Based on selection of individuals carrying genomic regions involved in the expression of the trait of interest
Marker assisted backcrossing (MABC)	Transfer of a limited number of loci from one genetic background to another
Marker assisted recurrent selection (MARS)	Markers associated with trait of interest are first identified and selection is based on several genomic regions involved in the expression of complex traits to assemble the most superior genotype within a population
Genome wide selection (GWS)	Based on the prediction of performance. Selection is made on markers without significance testing and does not require the prior identification of markers associated with the trait of interest

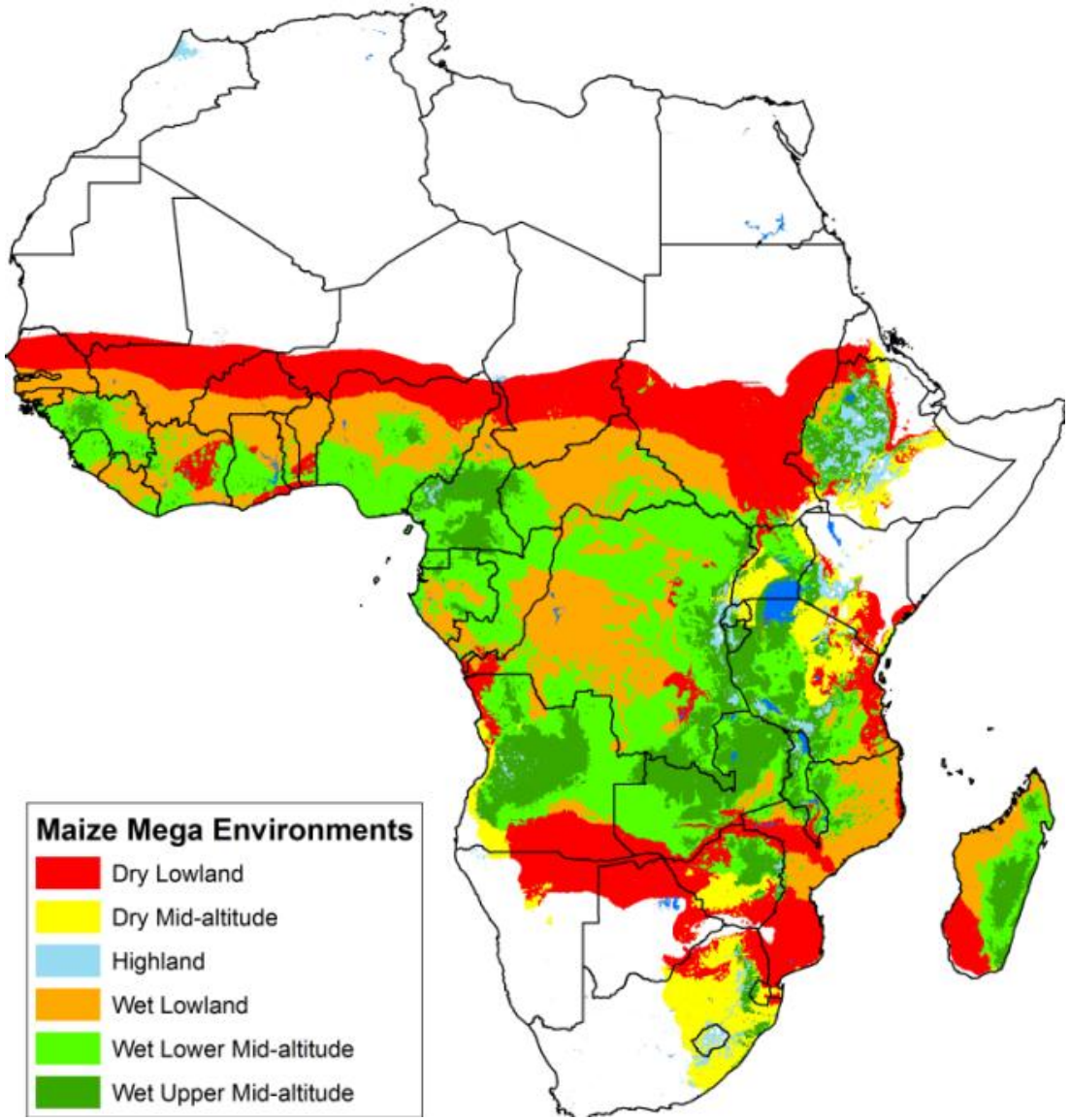

Figure 1. Maize mega-environments within sub-Saharan Africa (adapted from Hodson *et al.,* 2002a).

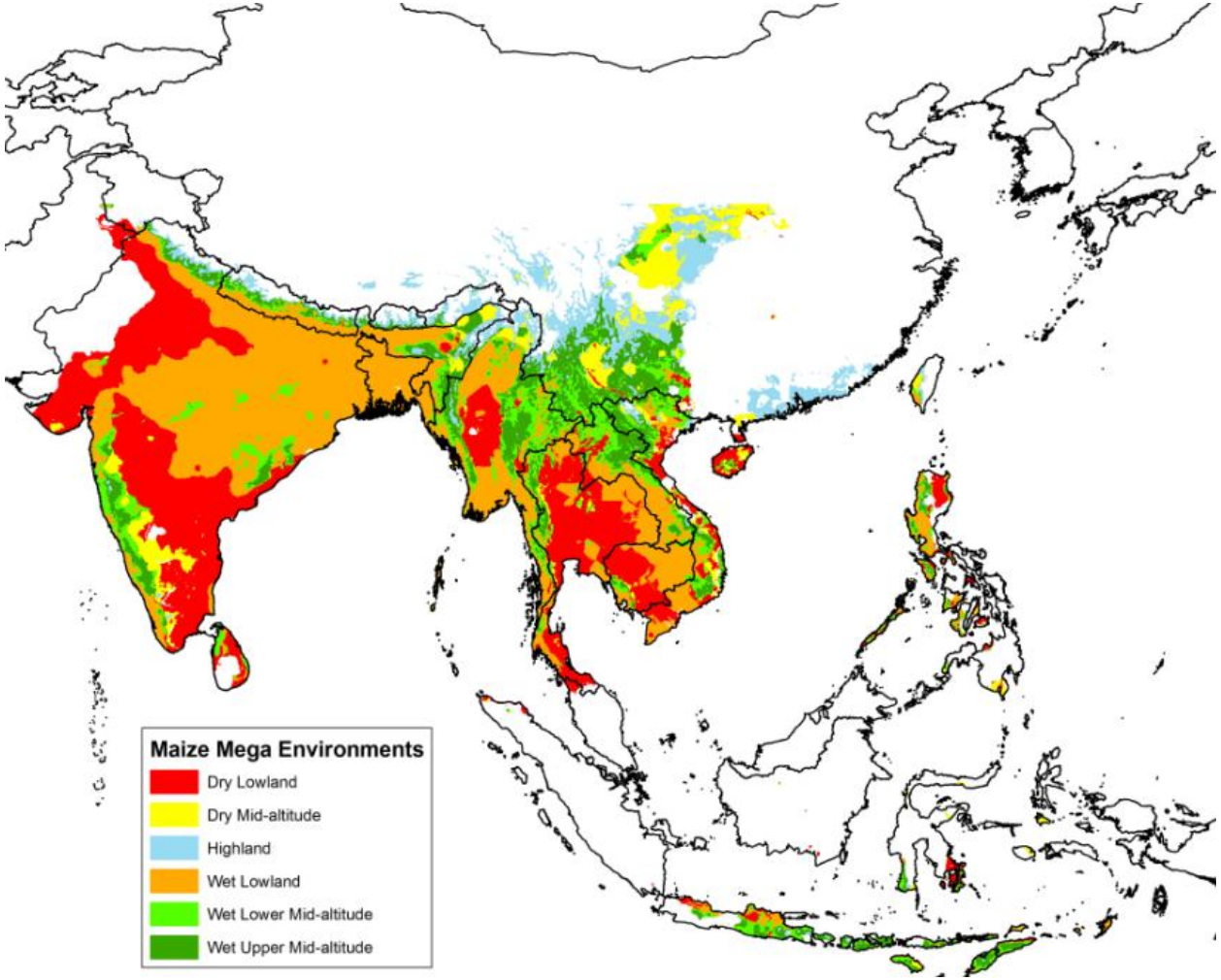

Figure 2. Maize mega-environments within Asia (adapted from Hodson *et al.,* 2002b).

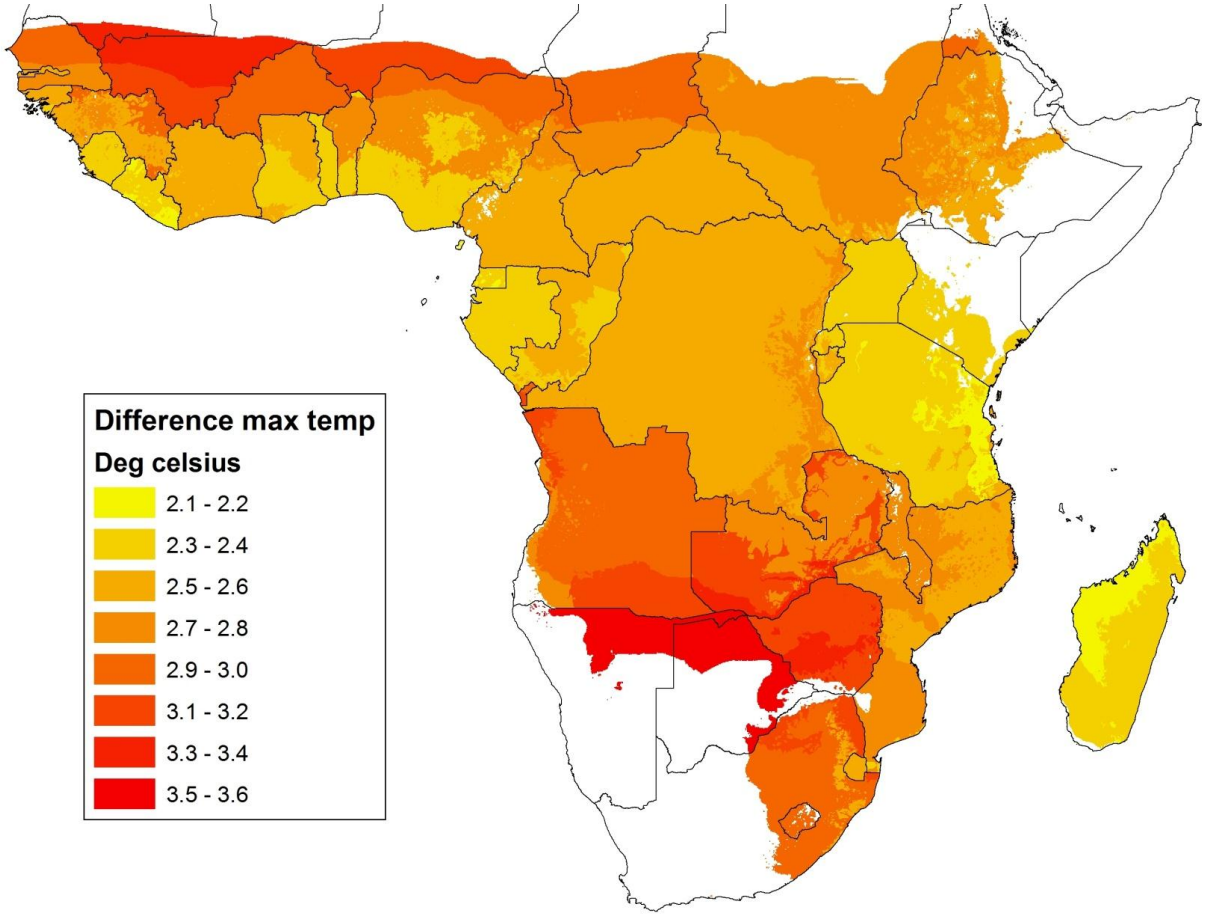

Figure 3. Increase in maximum temperatures in maize mega-environments in sub-Saharan Africa between 2050 and 1960-2000 using the outputs of 19 GCM's and A2 emissions scenarios.

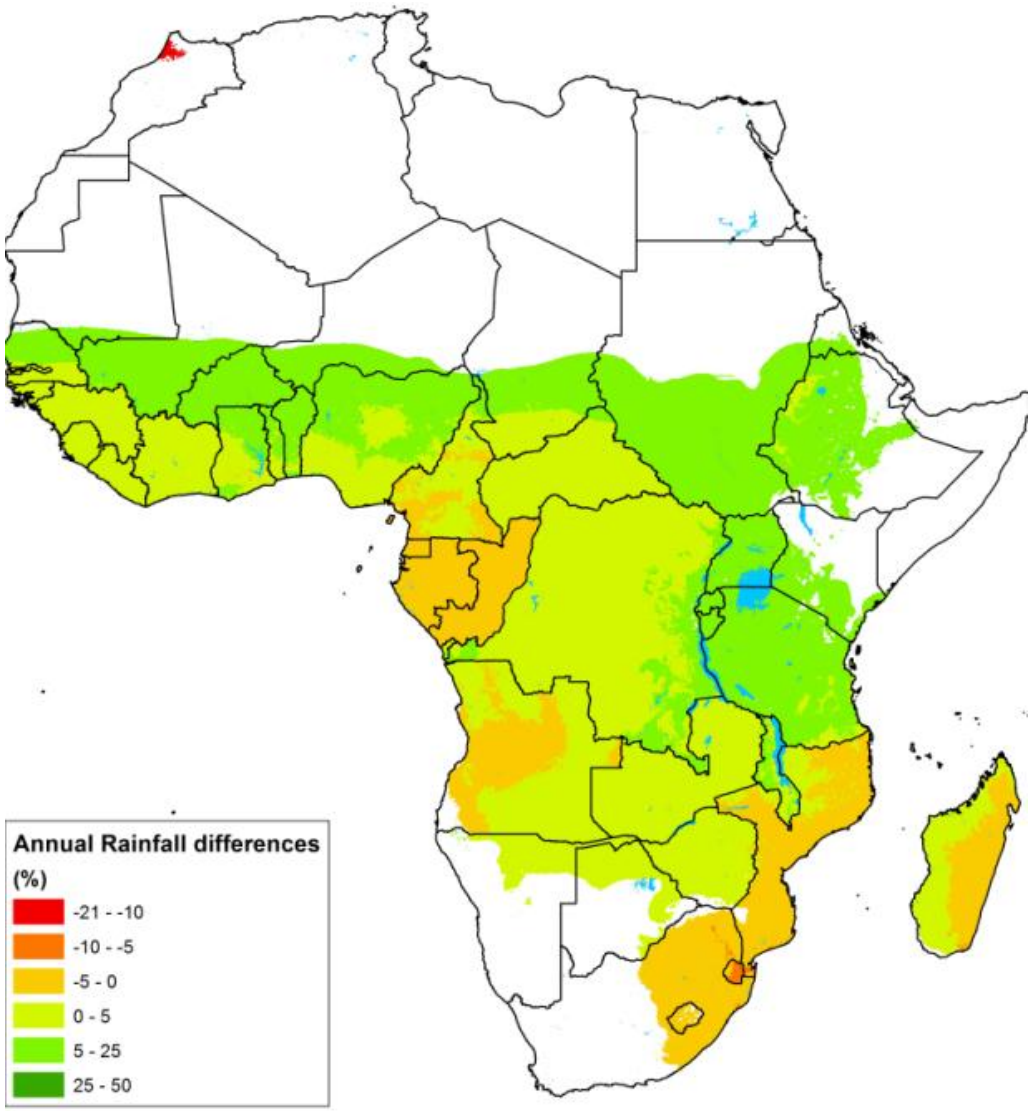

Figure 4. Differences in annual rainfall in maize mega-environments in sub-Saharan Africa between 2050 and 1960-2000 using the outputs of 19 GCM's and A2 emissions scenarios.

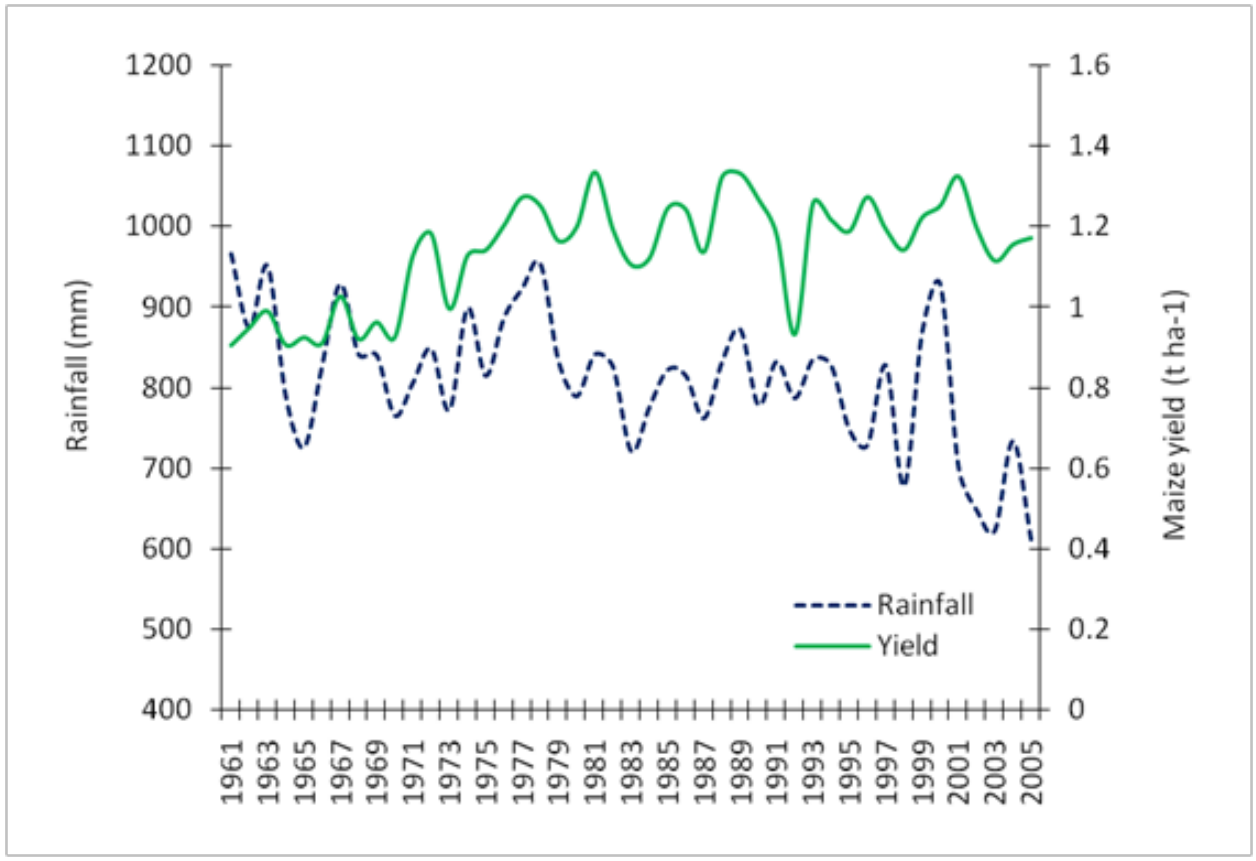

Figure 5. Relationship between rainfall and average maize yields across Eastern and Southern Africa (adapted from Bänziger and Diallo, 2001). Data source: FAOSTAT (2010) and Mitchell and Jones (2005).

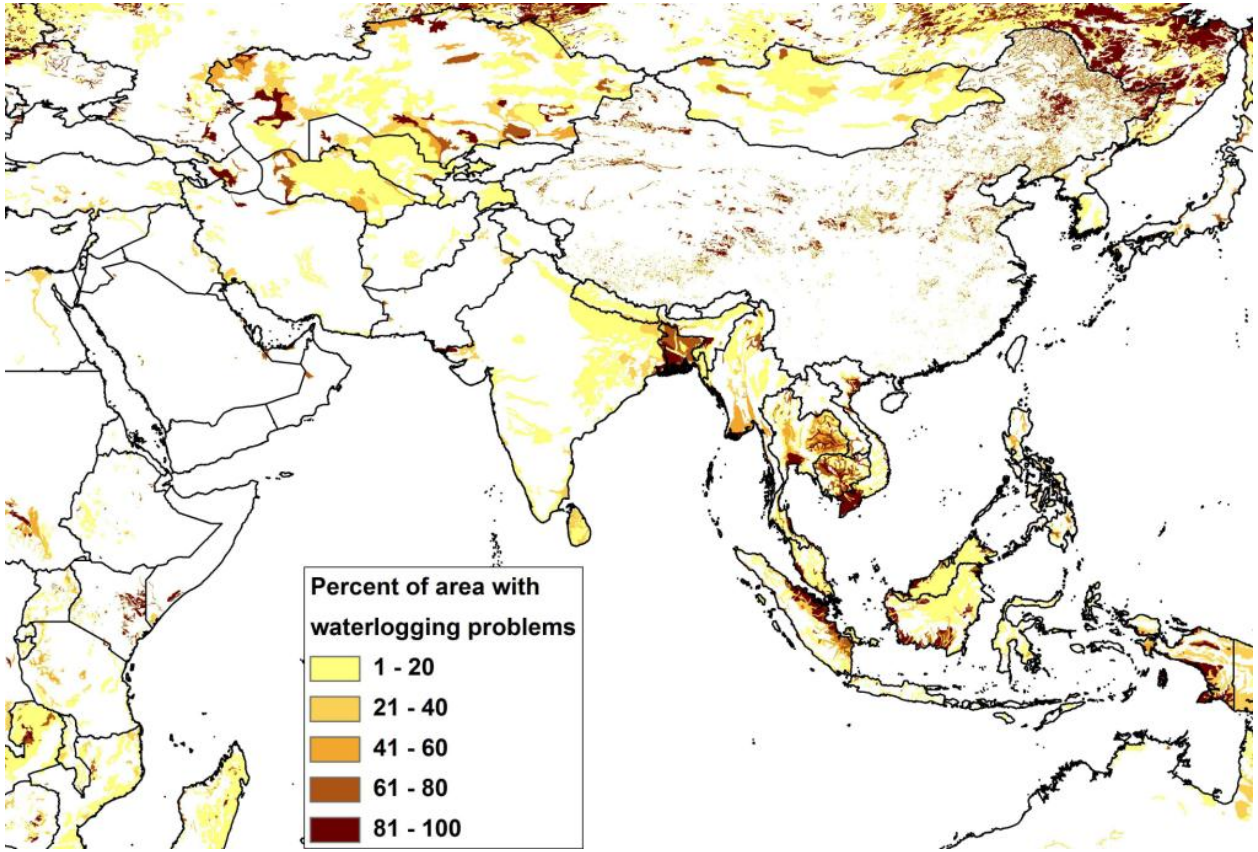

Figure 6. Water-logging risk in Asia. Datasource: Hodson *et al.,* (2002a), Sanchez *et al.,* (2003), *You et al.,* (2000) and You *et al.,* (2006),

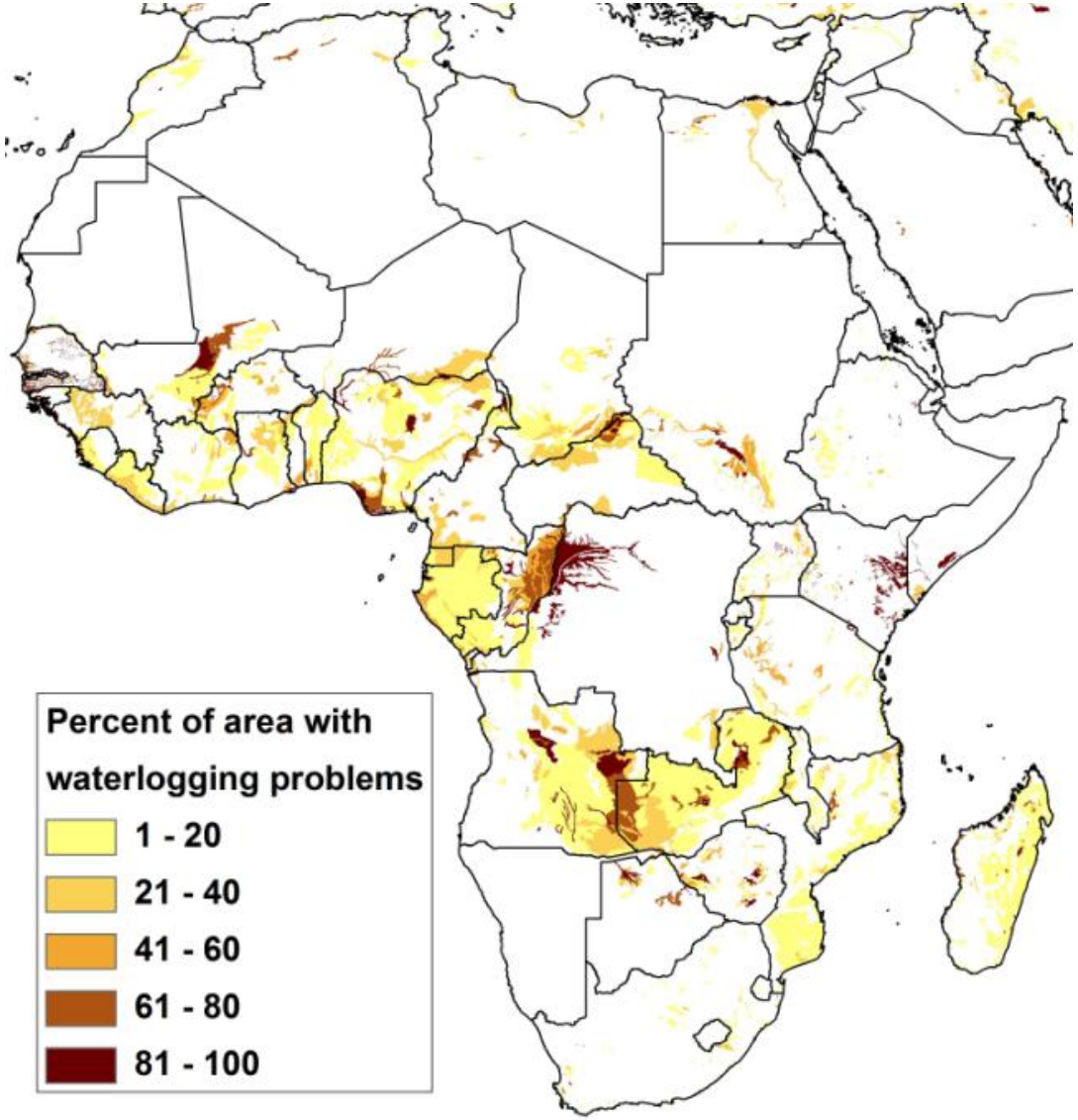

Figure 7. Water-logging risk in Africa . Datasource: Hodson *et al.,* (2002a), Sanchez *et al.,* (2003), *You et al.,* (2000) and You *et al.,* (2006),